

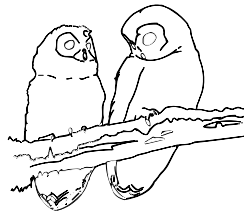
RANGE-WIDE STATUS AND TRENDS IN NORTHERN SPOTTED OWL POPULATIONS

Alan B. Franklin^{1,2}, Kenneth P. Burnham², Gary C. White³, Robert J. Anthony⁴, Eric D. Forsman⁵, Carl Schwarz⁶, James D. Nichols⁷, and James Hines⁷

12 April 1999

**Colorado Cooperative Fish and Wildlife Research Unit
United States Geological Survey - Biological Resources Division
Department of Fishery and Wildlife Biology
201 Wagar Building
Colorado State University
Fort Collins, CO 80523**

**Oregon Cooperative Fish and Wildlife Research Unit
United States Geological Survey - Biological Resources Division
Department of Fish and Wildlife
104 Nash Hall
Oregon State University
Corvallis, OR 97331-3803**



¹Department of Wildlife, Humboldt State University, Arcata, CA 95521

²Colorado Cooperative Fish & Wildlife Research Unit, Colorado State University, Fort Collins, CO 80523

³Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523

⁴Oregon Cooperative Fish and Wildlife Research Unit, Oregon State University, Corvallis, OR 97331

⁵U. S. Forest Service, Pacific Northwest Research Station, Corvallis, OR 97331

⁶Department of Statistics and Mathematics, Simon Fraser University, Burnaby, BC V5A 1S6, Canada

⁷Patuxent Wildlife Research Center, 11510 American Holly Drive, Laurel, MD 20708

ABSTRACT:

A workshop was held from 7-14 December 1998 to analyze demographic data on Northern Spotted Owls from 15 study areas in Washington, Oregon and Northern California. This workshop was the third in a series of large-scale analyses conducted on demographic data for the Northern Spotted Owl. Participants in the workshop included biologists from the different study areas, and analysts with expertise in analyzing demographic data. The study areas included in the analysis covered approximately 23% of the range of the Northern Spotted Owl, and were from studies on federal, Native American Tribal, and private lands. We analyzed demographic parameters (age-specific survival and fecundity) using capture-recapture estimators and mixed models, and annual rates of population change using projection matrices and a recent estimator developed by Pradel (1996) that used only the capture-recapture data. In addition to analyses for individual study areas, we also conducted two separate meta-analyses, one that included all 15 areas, and another that included only eight areas that were specifically identified in the Effectiveness Monitoring Plan for the Northern Spotted Owl. In these analyses, we also examined the data for any consistent trends over time. The results from the meta-analysis of survival indicated that annual survival probabilities of adult females varied among years, but did not exhibit a negative trend. This result differed from the 1993 meta-analysis (Burnham et al. 1994), which found a negative trend in adult female survival. Whether this change reflected a response to reductions in timber harvest rates on federal lands was unknown. Analyses on individual study areas corroborated the meta-analysis results except for three areas in California, which all exhibited significant negative trends in adult female survival. Fecundity varied among years, and did not exhibit any consistent linear trend; years of high and low reproduction tended to occur in alternate years, with highest reproduction in even-numbered years. This result was similar to the results of the 1993 analysis. Based on projection matrices, estimates of the annual rate of population change (λ) ranged from 0.828 to 0.984 for the individual study areas. Based on estimates of demographic parameters averaged across studies and juvenile survival corrected for emigration, we estimated an overall λ of 0.961 (95% confidence interval = 0.925 - 0.997) that indicated a 3.9% annual decline in the population of territorial females. Although the overall analysis indicated a declining population, some individual study areas had estimates of λ that did not differ from 1 (i.e., stationary populations) whereas other studies suggested substantial declines. We also explored an alternative model (Pradel 1996) for estimating λ that employed only capture-recapture data from selected studies. The results from this analysis suggested most of the selected study areas had stationary populations. However, three study areas exhibited negative trends in λ , indicating that annual rates of population change were declining on these areas, even though their average estimates of λ indicated stationary populations. The two methods of estimating λ differed in their interpretation and each had different biases related to sampling Northern Spotted Owls. Thus, there is still uncertainty regarding the health of the spotted owl population and we suggested several approaches to deal with this uncertainty in the future.

INTRODUCTION

The Northern Spotted Owl (*Strix occidentalis caurina*) is a medium-sized, nocturnal owl that inhabits coniferous forests of the Pacific Northwest, USA, and extreme southern British Columbia, Canada. The natural history of this species has been well documented because of its association with late-successional forests throughout its range (Forsman et al. 1984), which has led to considerable controversy about its management. Conservation of the Northern Spotted Owl and its habitat has been an extremely contentious issue among environmentalists, the timber industry, land managers, and scientists because of the size of its home range and the high economic value of trees within its habitat (Forsman and Meslow 1986, Thomas et al. 1990). This controversy has been a major natural resource issue in the Pacific Northwest for the last two decades because of the rapid logging of late-successional forests beginning around 1950. With the decline in late-successional forest, management options decreased, litigation increased, and a number of committees, task forces, and work groups were formed to find a biological and economical solution to the dilemma (Meslow 1993). The controversy became particularly intense in 1989 and 1990 when lawsuits halted the harvest of older forests on federal lands (e.g., Portland Audubon versus Lujan). In 1990, the Northern Spotted Owl was listed federally as a threatened species because suitable habitat was declining throughout its range, there was evidence of declining populations, and there were no regulatory mechanisms to protect the owl and its habitat (USDI 1990). At the center of the spotted owl-older forest controversy were questions about the status of their populations. To address these questions, a number of demographic studies on the species were initiated in the 1980's to estimate age-specific survival and fecundity rates and annual rates of population change (8). Because studies used similar field methods, efforts were made to analyze these studies collectively using similar analytical methods.

The first attempt to collectively analyze data from five demographic study areas was conducted in the form of a workshop (Anderson and Burnham 1992), the results of which were presented in the draft recovery plan for the species (USDI 1992). Analysis of demographic rates for Northern Spotted Owls and their interpretation have been the focus of much attention from both scientific and management perspectives. Recovery goals for the species focused on demographic performance (USDI 1992) of Northern Spotted Owls throughout their range, and demographic rates were the subject of much debate during the development of the Northwest Forest Plan for conservation of late-successional forests in the Pacific Northwest (FEMAT 1993). Most recently, demographic performance of Northern Spotted Owls has been incorporated in the Monitoring Plan for Implementation of the Pacific Northwest Forest Plan

(Lint et al. 1999).

A second analysis of demographic data for Northern Spotted Owls was conducted at a workshop in 1993 and included data from 14 study areas, seven of which had been initiated since the first workshop (Burnham et al. 1996). The data used in the second workshop were subjected to rigorous error checking before the workshop, and analytical philosophy, theory, and procedures were debated prior to starting the analysis. The three major findings from the second workshop were: 1) fecundity rates varied by age-classes and time, with no increasing or decreasing trends over time, 2) survival rates were age-dependent and there was a decreasing trend in adult female survival, and 3) the annual rate of population change (λ) was significantly less than one for 10 of 11 areas (Burnham et al. 1996). In addition, a meta-analysis across studies estimated that Northern Spotted Owl populations were declining at a rate of about 5% per year during the time period when the studies were conducted. One of the most important results from this workshop was the decline in adult female survival because the population projection matrices used to estimate λ were most sensitive to changes in adult female survival (Lande 1988, Noon and Biles 1990).

This report summarizes the results of a third workshop which was convened in December 1998 to analyze data on demographic rates of Northern Spotted Owls. Our primary goal was to address two major questions. First, we asked: *were there consistent trends in age-specific survival and fecundity rates across the range of the Northern Spotted Owl?* Second, we asked: *if there were consistent trends in the annual rates of population change across the range of the owl?* In addition, we were particularly interested in whether the decline in adult female survival rates had continued, because such a decline over a ≥ 10 year period would be cause for concern. The process and protocol for data analysis established in previous workshops (see Anderson and Burnham 1992, Burnham et al. 1996) were repeated in the analysis of data from 16 study areas. The objectives of our analyses were to:

- 1) estimate age-specific survival probabilities and fecundity rates, and their sampling variances, for individual study areas;
2. estimate range-wide trends in adult female survival and fecundity across study areas;
- 3) estimate annual rates of population change (λ), and their sampling variances, for individual study areas and across study areas based on Leslie projection matrices; and
- 4) explore an alternative approach for estimating rates of annual population change using a capture-recapture estimator based on the reparameterized Jolly-Seber model (Pradel 1996).

We were particularly interested in examining the hypothesis that owl populations were “stationary” ($\delta = 1$) during the period of study versus the alternative that populations were declining ($\delta < 1$). Herein, we report the results of these analyses with the purpose of describing the status and trends of Northern Spotted Owl populations throughout most of the range of this subspecies.

STUDY AREAS

The analysis included data from 16 study areas in Washington, Oregon and northwestern California (Table 1). However, one of the study areas (COA) was part of another study area (ELC). Therefore, COA was excluded from analyses across study areas although we reported estimates from this study area for individual study area analyses. Thus, our results are generally limited to 15 study areas (Fig. 1) unless noted. The combined area of the 15 study areas was 52,953 km² (Table 1), which included about 23% of the 230,690 km² range of the Northern Spotted Owl (USDA and USDI 1994). Two of the study areas were on private lands, two were on Native American Tribal lands, one was on Oregon Department of Forestry lands, and 10 were on areas dominated by U. S. Forest Service (USFS), Bureau of Land Management (BLM), U. S. National Park Service (NPS), or State lands (Table 1). Study areas on BLM Districts (KLA, TYE, EEU, and portions of ELC in Fig. 1) typically included a "checker-board" ownership pattern in which square-mile sections of BLM lands alternated with sections of private land. In contrast, land ownership on USFS and NPS study areas was mostly federal, with only small inclusions of private or state land.

Our study areas differed from those in the previous analysis by Burnham et al. (1994, 1996) in several ways. First, we added six new study areas (RAI, WSR, AST, EEU, HUP, SIM), and we included five additional years of data from areas evaluated in the earlier analysis. In addition, our study differed from Burnham et al. (1994, 1996) in that some of their study areas were dropped or reconfigured in 1994-1996 to conform to a long-term monitoring plan adopted by the U. S. Forest Service and Bureau of Land Management (Lint et al. 1999). In particular, study areas on all BLM Districts in western Oregon were reduced in size in 1994-1996, and one

TABLE 1. Characteristics of 16 Northern Spotted Owl demographic study areas in Oregon, Washington, and California. Starred areas are those used in effectiveness monitoring.

Study Area	State	Acronym	Organization conducting study	Study period (No.of years)	No. capture histories	Approximate size (km ²)
Astoria State Forest	OR	AST	OCWRU ^a	1991 - 1998 (8)	47	358
*Southern Cascades	OR	CAS	OCWRU ^a	1991 - 1998 (8)	446	2,590
*Cle Elum	WA	CLE	USFS ^b	1989 - 1998 (10)	589	1,784
*Oregon Coast Range ^c	OR	COA	USFS/BLM ^d	1990 - 1998 (9)	772	3,918
Elliott St. Forest & COA	OR	ELC	USFS/ BLM/ OCWRU	1990 - 1998 (9)	853	4,295
East Eugene	OR	EEU	NCASI ^e	1990 - 1998 (9)	179	2,537
*H. J. Andrews	OR	HJA	OCWRU	1987 - 1998 (12)	751	1,526
Hoopa Tribal Lands	CA	HUP	Hoopa Tribal Council	1992 - 1998 (7)	188	356
*Roseburg BLM - Klamath	OR	KLA	BLM	1985 - 1998 (14)	742	1,377
*NW California	CA	NWC	Humboldt State University	1985 - 1998 (14)	795	1,790
*Olympic Peninsula	WA	OLY	USFS/NPS ^f	1987 - 1998 (12)	869	8,152
Rainier	WA	RAI	Raidecke Associates	1992 - 1998 (7)	143	2,133
Simpson	CA	SIM	Simpson Timber Company	1990 - 1998 (9)	1011	1,265
*Roseburg BLM - Tyee	OR	TYE	BLM	1985 - 1998 (14)	737	1,741
Wenatchee	WA	WEN	NCASI	1990 - 1998 (9)	957	22,048
Warm Springs Tribal Lands	OR	WSR	Warm Spings Tribal Council	1992 - 1998 (7)	318	1,001

^aOregon Cooperative Fish and Wildlife Research Unit

^bU. S. Forest Service

^cNot included in meta-analysis of single studies because was included in ELC data.

^dBureau of Land Management

^eNational Council for Air and Stream Improvement

^fNational Park Service

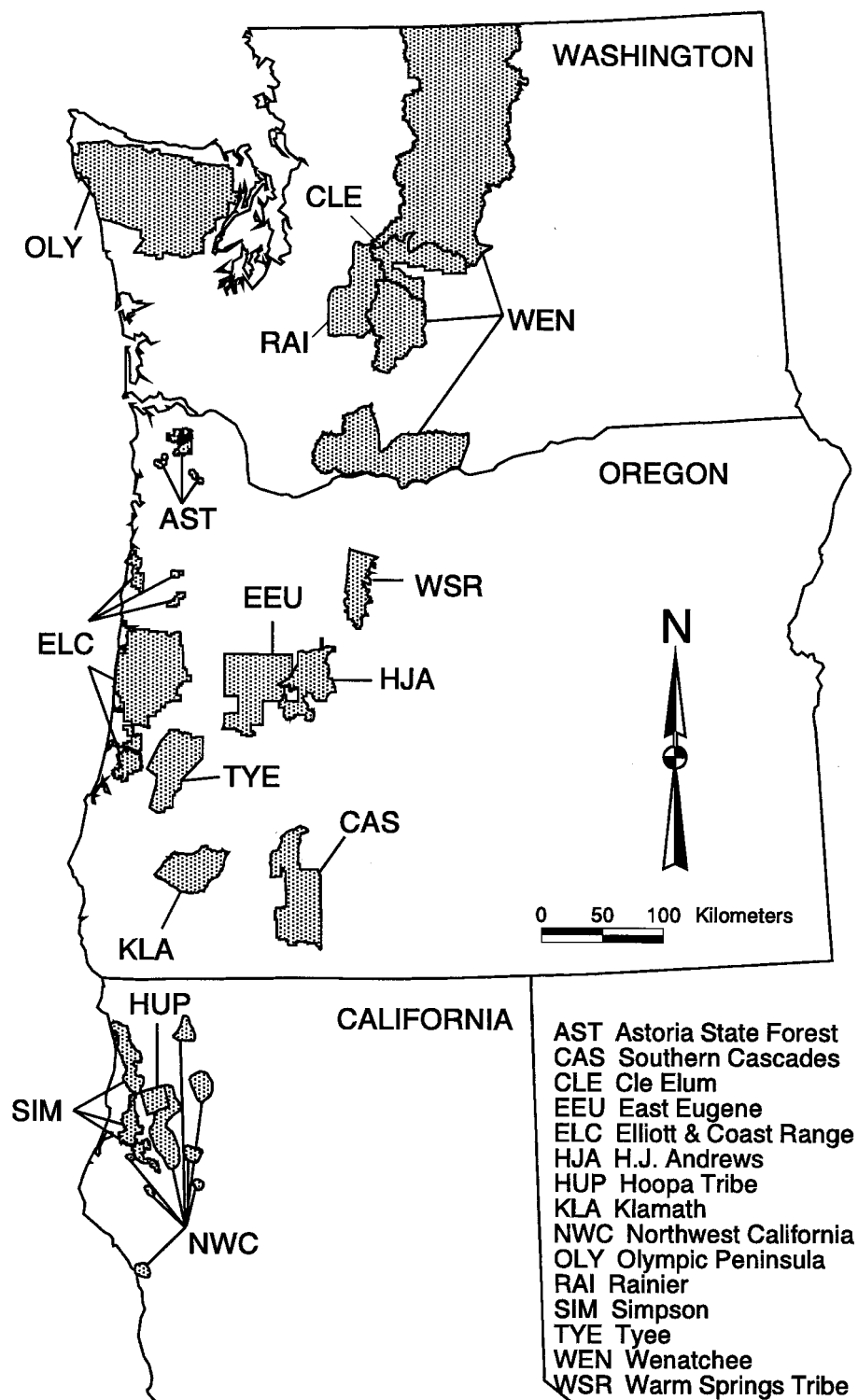


FIGURE 1. Map showing the location of the 15 Northern Spotted Owl demographic study areas from which data were analyzed. The COA study area was included as part of ELC study area.

small study on the Siskiyou National Forest was discontinued in 1994. Our analysis only included the reconfigured study areas that were surveyed through 1998. These changes can be examined by comparing Fig.1 of this report to Fig. 1 in Franklin et al. (1996:13). Selection of study areas by the federal, state and private groups that participated in the analysis was based on many considerations, including logistics, funding, and land ownership boundaries. As a result, study areas were not randomly or systematically spaced across the landscape. Nevertheless, it was the consensus of the workshop participants that the broad distribution of study areas on federal lands was representative of the overall condition of spotted owl populations on federal lands (Fig. 1). Because coverage of state and private lands was less extensive, and because management practices vary widely on private lands, participants were less certain whether the results were generally applicable to state and private lands.

METHODS

The demographic parameters of interest were age-specific survival probabilities and age-specific fecundity. Empirical data sets from each study area consisted of 1) capture histories for each banded individual along with information on sex and age-class (juvenile, 1-year olds, 2-year olds, and adults), and 2) a data file with records of annual reproductive output (number of juveniles fledged) for females. A number of people with special expertise in capture-recapture analysis, population dynamics theory, and statistical science were invited to supervise the analyses (Appendices A and B), and every effort was made to assure the integrity of the analyses and inferences.

Quality controls were established at all levels of the workshop. First, empirical data from each of the study areas were subjected to a formal error-checking process where ten records were randomly drawn from each data set. Investigators from each study area were then required to provide field data forms to verify the selected records. Second, data were formally certified prior to analysis by each investigator who signed a form stating that the data had been verified through the error-checking process and that data would not be subsequently changed or withdrawn from the workshop analysis. Third, bootstrap goodness-of-fit tests (see Estimation of Survival) were performed on the capture-recapture data before the workshop was convened. Fourth, *a priori* analysis protocols were established by the entire group of investigators and analysts and agreed upon during the workshop (Appendix C). Considerable formal theory and computer software existed to guide the analysis. The basis for the statistical analyses was rooted in standard likelihood theory and methods, and in current philosophy of parametric statistical

analysis of large, inter-related data sets. Direct inferences were limited to the years for which data were available. Because of the number, large size, and wide distribution of the study areas, we made statistical inferences beyond the specific study areas to the range of the Northern Spotted Owl.

ESTIMATION OF SURVIVAL

Age-specific survival was estimated from capture-recapture data where “recapture” referred to either physical recapture of marked individuals or resighting of color marks on individuals (see Franklin et al. 1996, Forsman et al. 1996). We used open population capture-recapture models to estimate age-specific survival rates for each study area. In addition to age-specific survival estimates for each study area, a meta-analysis was conducted for adult female survival with two separate analyses. The first meta-analysis included the 15 individual study areas, while the second included eight of the individual areas that were specifically identified as long-term monitoring areas by Lint et al. (1999).

Capture-recapture analysis of the spotted owl data allowed estimation of annual apparent survival probabilities (N_t ; probability that an owl alive in a particular year t , survives to the same time next year ($t+1$) and remains on the study area and, hence, is available for recapture) and recapture probabilities (p ; probability that an animal alive in year t is captured, or recaptured). The basic data were the capture histories of all individuals caught and banded along with the sex, age-class, and study area where the owl was located. Given sufficient sample sizes, one can estimate (in principle) yearly survival probabilities (roughly from 15 June one year to the next 15 June) for males and females, and for juvenile (J), 1-year old (S1), 2-year old (S2), and adult (A; ≥ 3 years old) age classes (see Forsman et al. 1983, Moen et al. 1991 and Franklin et al. 1996) for complete descriptions of ageing and sexing techniques). The estimation of survival from capture-recapture data for Northern Spotted Owls has been explicitly described elsewhere (Burnham et al. 1993, Burnham et al. 1996, Franklin et al. 1996) and will not be reiterated here. Instead, we will describe the approach used and discuss new analytical methods applied to the current data that differ from previous analyses.

The general approach used to analyze the capture-recapture data for survival estimates was to: 1) evaluate goodness-of-fit and estimate an over-dispersion parameter (c) for each data set, 2) determine a set of *a priori* models to analyze, 3) analyze each capture-recapture data set with the *a priori* models using program MARK (White and Burnham 1999), 4) adjust the covariance matrices and AICc values with \hat{c} to obtain QAICc values and 5) select an appropriate

model for inference based on QAICc model selection (Burnham and Anderson 1998). Details of this approach are presented in the following sections.

Individual Study Area Analyses

The focus of the data analysis and model selection process for each study area was to find the capture-recapture model that best fit the data, i.e., the most "parsimonious" model. Prior to model fitting we used a parametric bootstrap procedure on the global model $\{N_{st\ at\ t}, p_{st\ at\ t}\}$ to test the goodness-of-fit of each data set to the assumptions of the Cormack-Jolly-Seber model (Cormack 1964, Jolly 1965, Seber 1965, Burnham et al. 1987, Pollock et al. 1990, Franklin et al. 1996). The global model included estimates for age, sex, and time effects, plus interactions between these effects for both N and p .

The bootstrap analysis was conducted in Program MARK (White and Burnham 1999). With this procedure, estimates from the model being evaluated are used to generate simulated data that exactly meet the assumptions of the Cormack-Jolly-Seber model, i.e., no overdispersion is included, animals are totally independent, and no violations of model assumptions are included. Data are simulated based on the number of animals released at each occasion, and a simulated capture history is constructed for each release. Once capture histories were generated, the numerical estimation procedure was run to compute the deviance and its degrees of freedom. These values were saved and the entire process was repeated 500 times. Deviances of the simulated data were then ranked in ascending order, and the relative rank of the deviance from the original data was used to estimate a P -value. An estimate of overdispersion (c) was obtained by dividing the deviance estimate from the original data by the mean of the simulated deviances. The mean of the simulated deviances represents the expected value of the deviance under the null model of no violation of assumptions. Thus, \hat{c} here provided a measure of the amount of over-dispersion in the original data, and can be used to correct for violations of assumptions that result in overdispersion, such as with the use of a quasi-likelihood variance inflation (Burnham et al. 1987, Lebreton et al. 1992, Burnham and Anderson 1998).

Once c was estimated and the results from the initial global model corrected for any overdispersion, further analysis involved fitting a series of candidate models (Table 2) that were chosen *a priori* during the workshop protocol sessions (Appendix C). These candidate models allowed N and p to vary by time (t), or have linear (T) or non-linear constraints to estimate trends over time. The non-linear structures were applied only to N and were either pseudo-threshold or quadratic structures. The pseudo-threshold ($\ln T$) structure predicted that effects changed at a

TABLE 2. *A priori* models, and their descriptions, developed for analysis of apparent survival (\mathcal{N}) and recapture probability (p) for each of the individual study areas. Age-classes denoted as J for juveniles, S1 for 1-year olds, S2 for 2-year olds and A for adults. NJ indicates non-juveniles where S1, S2 and A classes were combined.

Model ^a	Description
1. $\{\mathcal{N}_{a*s*t}, p_{a*s*t}\}$	\mathcal{N}, p : age, sex, and time effects and all interactions (global model).
2. $\{\mathcal{N}_{[J, [S1, S2, A]+s]+t}, p_{[a4'+s], [NJ+s+T]}\}$	\mathcal{N} : age effect; additive sex effect for S1, S2, and A; additive time effect for all ages. p : additive sex effect for a4' juveniles; additive sex and time effects for non-juveniles.
3. $\{\mathcal{N}_{[J, [S1, S2, A]+s]+t}, p_{[a4'+s], [NJ+s+T]}\}$	\mathcal{N} : same as model 2. p : same as model 2 except that time effect is a linear trend.
4. $\{\mathcal{N}_{[J, [S1, S2, A]+s]+t}, p_{[a4'+s], [NJ+s]}\}$	\mathcal{N} : same as model 2. p : same as model 2 except that there is no time effect.
5. $\{\mathcal{N}_{[J, [S1, S2, A]+s]+t}, p_{\text{choice 1}}\}$	\mathcal{N} : same as model 2. p : biologists choose a model specific to their study areas, e.g., include survey effort, fecundity covariates, etc..
6. $\{\mathcal{N}_{[J, [S1, S2, A]+s]+t}, p_{\text{choice 2}}\}$	\mathcal{N} : same as model 2. p : biologists choose a second model specific to their study areas.
7. $\{\mathcal{N}_{[J, [S1, S2, A]+s]+t}, p_{\text{choice 3}}\}$	\mathcal{N} : same as model 2. p : biologists choose a third model specific to their study areas.
8. $\{\mathcal{N}_{[J, NJ+s]+t}, p_{[a4'+s], [NJ+s+T]}\}$	\mathcal{N} : age effect; additive sex effect for non-juveniles; additive time effect for both age groups. p : same as model 2.
9. $\{\mathcal{N}_{[J, NJ+s]+t}, p_{[a4'+s], [NJ+s+T]}\}$	\mathcal{N} : same as model 8. p : same as model 3.
10. $\{\mathcal{N}_{[J, NJ+s]+t}, p_{[a4'+s], [NJ+s]}\}$	\mathcal{N} : same as model 8. p : same as model 4.
11. $\{\mathcal{N}_{[J, NJ+s]+t}, p_{\text{choice 1}}\}$	\mathcal{N} : same as model 8. p : same as model 5.
12. $\{\mathcal{N}_{[J, NJ+s]+t}, p_{\text{choice 2}}\}$	\mathcal{N} : same as model 8. p : same as model 6.
13. $\{\mathcal{N}_{[J, NJ+s]+t}, p_{\text{choice 3}}\}$	\mathcal{N} : same as model 8. p : same as model 7.
14. $\{\mathcal{N}_{[J, NJ+s]+T}, p_{\text{best from 1-13}}\}$	\mathcal{N} : age effect; additive sex effect for non-juveniles; additive linear time trend for both age groups. p : same as whichever model from models 1-13 resulted in the lowest QAICc value.
15. $\{\mathcal{N}_{[J, NJ+s]+lnT}, p_{\text{best from 1-13}}\}$	\mathcal{N} : same as model 14 except that the time trend is logarithmic. p : same as model 14.
16. $\{\mathcal{N}_{[J, NJ+s]+[TT]}, p_{\text{best from 1-13}}\}$	\mathcal{N} : same as model 14 except that the linear time trend has an additional quadratic term. p : same as model 14.
17. $\{(\mathcal{N}, p)_{\text{best from 1-16 without sex effect for } \mathcal{N}}\}$	\mathcal{N}, p : same as whichever model from models 1-16 resulted in the lowest QAICc value, without a sex effect for \mathcal{N} .
18. $\{(\mathcal{N}, p)_{\text{best from 1-17 with juvenile } \mathcal{N}_{\text{constant}}}\}$	\mathcal{N}, p : same as whichever model from models 1-17 resulted in the lowest QAICc value, without a time effect on juvenile survival.

^a Model subscripts indicate age (a), sex (s) or time (t , T) effects. An $a4'$ indicates that birds initially banded as juveniles have different recapture rates over three years following first capture than birds initially banded as non-juveniles. Time effects varied by year (t), or were linear (T), logarithmic (lnT) or quadratic (TT).

constant rate to some point and then approached (but did not reach) an asymptote, and a quadratic structure (TT) predicted some maximum at intermediate years and lower effects at early and late years (Franklin 1997).

Model fitting and optimal parameter estimation was done using maximum likelihood estimation. We used QAICc for model selection (Lebreton et al. 1992, Burnham and Anderson 1998). QAICc is a version of Akaike's Information Criterion (Akaike 1973 and 1985, Sakamoto et al. 1986) that is corrected for small sample bias (Hurvich and Tsai 1989) and over-dispersion (Lebreton et al. 1992, Anderson and Burnham 1994). QAICc was computed as per Burnham and Anderson (1998:53):

$$QAICc = \frac{-2 \log(Likelihood)}{\hat{c}} + 2K + \frac{2K(K + 1)}{n_{ess} - K - 1},$$

where the log-likelihood is evaluated at the maximum likelihood estimates under a given model, K is the number of estimable parameters in the model, \hat{c} is the estimated quasi-likelihood variance inflation for overdispersion, and n_{ess} is the effective sample size (number of releases for the capture-recapture data). QAICc was computed for each candidate model and the best model for inference was the model with the minimum QAICc value. Two additional tools based on QAICc values were also computed for each model, Δ_i (where $\Delta_i = QAICc_i - \min QAICc$) and Akaike weights (Buckland et al. 1997, Anderson and Burnham 1998). Akaike weights were computed over a set of R models based on Δ_i as:

$$w_i = \frac{e^{-\left(\frac{\Delta_i}{2}\right)}}{\sum_{r=1}^R e^{-\left(\frac{\Delta_r}{2}\right)}}$$

Akaike weights were used to address model selection uncertainty and the degree to which ranked models were considered competitive. The selected model, and the associated maximum likelihood estimates of the parameters, provided the best inference from the data.

We used a variance components analysis (Burnham et al. 1987) to estimate spatial process variation ($\sigma_{spatial}^2$) in N and mean annual estimates of N across study areas. This approach allowed us to account for sampling variation in parameter estimates when estimating spatial process variation. Mean annual fecundity and annual rates of population change were estimated in a similar manner except where noted.

Estimation of Undetected Emigration Rates for Adjusting Juvenile Survival Estimates

To estimate mean annual emigration rates (\hat{E}) of juvenile owls we used radio-tracking data from 154 juveniles on the TYE ($n = 105$), OLY ($n = 19$) and CLE ($n = 30$) study areas (E. Forsman, unpublished data). For this analysis, \hat{E} was defined as the probability that a juvenile moved off the study area where it was banded, survived until the following year, and was not recaptured. We estimated \hat{E} according to Burnham et al. (1994) as:

$$\hat{E} = \frac{n_{en}}{n}, \text{ with } \hat{se}(\hat{E}) = \sqrt{\frac{\hat{E}(1-\hat{E})}{n}},$$

where n was the total number of survivors in the spring of year $t+1$ of the owls that were radio-marked in the summer of year t , and n_{en} was the number that emigrated off the natal study area, survived the year, and were not detected by capture-recapture methods.. The total number of survivors (n) could be re-written as $n = n_s + n_{ed} + n_{en}$ where n_s was the number that remained in their natal study area and survived the year, and n_{ed} was the number that emigrated from their natal study area, survived the year, and were detected by capture-recapture methods without the aid of radio-telemetry. All of these quantities were estimated from the radio-marked juveniles. Our estimate of (\hat{E}) assumed that all emigration occurred by 1 April of year $t+1$, and that subsequent mortality rates were the same for emigrants and non-emigrants (Burnham et al. 1994). Apparent survival estimates for juveniles ($\hat{\phi}_0$) were adjusted by \hat{E} to estimate true juvenile survival (\hat{S}_0) as:

$$\hat{S}_0 = \frac{\hat{\phi}_0}{1 - \hat{E}} \text{ with } \hat{var}(\hat{S}_0) = (\hat{S}_0)^2 \left[[CV(\hat{\phi}_0)]^2 + [CV(1 - \hat{E})]^2 \right]$$

Covariances between \hat{S}_0 and $\hat{\phi}_x$ (where x = other age-classes) were estimated as:

$$\hat{cov}(\hat{S}_0, \hat{\phi}_x) = \frac{\hat{cov}(\hat{\phi}_0, \hat{\phi}_x)}{1 - \hat{E}}$$

Meta-analysis of Trends in Annual Survival of Adult Females

Adult female capture histories from each of the 15 study areas were combined to perform the survival meta-analysis for adult females. For each study area, zeros were added to the beginning of the capture history so that capture histories for each study area were the same length (i.e., the first column of all capture histories started on the same calendar year). For each study area, capture histories included owls initially banded as adult females along with the relevant portions of capture histories for females initially banded as juveniles, 1-, and 2-year old

owls. That is, for juvenile females, the portion of their capture history representing juvenile, 1-year old and 2-year old age-classes was set to zeros and only the portion of their capture history when they were adults was included. Equivalent procedures were used for birds initially banded at 1- and 2-year old ages. Study area was treated as an attribute group variable in program MARK.

We evaluated goodness-of-fit for the global model $\{N_{g^*t}, p_{g^*t}\}$ using the parametric bootstrap procedure described for the individual study areas analyses. For apparent survival rates, we considered the models with N_{g^*t} , N_{g+t} , N_{g^*T} , and N_{g+T} , where g represents study area. In addition, we considered the following models for recapture probability: p_{g^*t} , p_{g+t} , p_{g^*T} , and p_{g+T} . When combined with the four models of apparent survival, a list of 16 models resulted (Table 3). For the best model resulting from analysis of the models in this list, we replaced the study area effect of apparent survival by the following four variables to create four additional models: ecological province, land ownership, ecological province*land ownership interaction, and latitude.

Data were subdivided into four broad ecological provinces as follows: East Slope Cascades (CLE, WEN, WSR); Douglas Fir/Hemlock (AST, OLY, RAI, HJA, ELC, EEU, TYE); Mixed Conifer/Hardwood (CAS, NWC, KLA, HUP); and Redwood (SIM). Each study area was assigned to a land ownership category based on predominant land ownership within the area as follows: U. S. Forest Service /National Park Service (included CAS, HJA, NWC, OLY); Mixed Ownership (ELC, KLA, TYE, EEU, CLE, RAI, WEN); and Non-Federal Ownership (AST, HUP, WSR, SIM). Latitude was treated as a continuous variable (i.e., a trend variable). Identical procedures were used for the 8 monitoring areas to construct a meta-analysis for just those areas. Model selection procedures for the meta-analyses were the same as for individual study area analyses.

ESTIMATION OF FECUNDITY

Data collection involved monitoring territorial females to determine their annual reproductive output (number of young fledged) (see Forsman 1983 and Franklin et al.. 1996). For each territorial female, the number of young fledged, the study area, the site (territory) within each study area where the young were detected, the year of the study, and the age of the female (1-year old, 2-year old or adult) were recorded. One problem in estimating fecundity over time was the confounding between individuals and territories caused by females breeding on the same

TABLE 3. *A priori* models, and their descriptions, developed for meta-analysis of apparent survival (\mathcal{N}) and recapture probability (p) of adult female Northern Spotted Owls.

Model ^a	Description
1. $\{\mathcal{N}_{g*t}, p_{g*t}\}$	\mathcal{N} : study area and time effects with all interactions. p : study area and time effects with all interactions.
2. $\{\mathcal{N}_{g*t}, p_{g+t}\}$	\mathcal{N} : study area and time effects with all interactions. p : additive study area and time effects.
3. $\{\mathcal{N}_{g*t}, p_{g*T}\}$	\mathcal{N} : study area and time effects with all interactions. p : study area effects, a linear time trend, and all interactions.
4. $\{\mathcal{N}_{g*t}, p_{g+T}\}$	\mathcal{N} : study area and time effects with all interactions. p : additive study area effects with a linear time trend.
5. $\{\mathcal{N}_{g+t}, p_{g*t}\}$	\mathcal{N} : additive study area and time effects. p : same as model 1.
6. $\{\mathcal{N}_{g+t}, p_{g+T}\}$	\mathcal{N} : additive study area and time effects. p : same as model 2.
7. $\{\mathcal{N}_{g+t}, p_{g*T}\}$	\mathcal{N} : additive study area and time effects. p : same as model 3.
8. $\{\mathcal{N}_{g+t}, p_{g+T}\}$	\mathcal{N} : additive study area and time effects. p : same as model 4.
9. $\{\mathcal{N}_{g*T}, p_{g*t}\}$	\mathcal{N} : study area effects, a linear time trend, and all interactions. p : same as model 1.
10. $\{\mathcal{N}_{g*T}, p_{g+T}\}$	\mathcal{N} : study area effects, a linear time trend, and all interactions. p : same as model 2.
11. $\{\mathcal{N}_{g*T}, p_{g*T}\}$	\mathcal{N} : study area effects, a linear time trend, and all interactions. p : same as model 3.
12. $\{\mathcal{N}_{g*T}, p_{g+T}\}$	\mathcal{N} : study area effects, a linear time trend, and all interactions. p : same as model 4.
13. $\{\mathcal{N}_{g+T}, p_{g*t}\}$	\mathcal{N} : additive study area effects with a linear time trend. p : same as model 1.
14. $\{\mathcal{N}_{g+T}, p_{g+T}\}$	\mathcal{N} : additive study area effects with a linear time trend. p : same as model 2.
15. $\{\mathcal{N}_{g+T}, p_{g*T}\}$	\mathcal{N} : additive study area effects with a linear time trend. p : same as model 3.
16. $\{\mathcal{N}_{g+T}, p_{g+T}\}$	\mathcal{N} : additive study area effects with a linear time trend. p : same as model 4.
17. $\{\mathcal{N}_{\text{prov*best from 1-16}}, p_{\text{best from 1-16}}\}$	\mathcal{N} : province and best model from 1-16 effects with all interactions. p : same as whichever model from models 1-16 resulted in the lowest QAICc value.
18. $\{\mathcal{N}_{\text{owner*best from 1-16}}, p_{\text{best from 1-16}}\}$	\mathcal{N} : ownership and best model from 1-16 effects with all interactions. p : same as model 17.
19. $\{\mathcal{N}_{\text{prov*owner*best from 1-16}}, p_{\text{best from 1-16}}\}$	\mathcal{N} : province, ownership, and best model from 1-16 effects with all interactions. p : same as model 17.
20. $\{\mathcal{N}_{\text{g[latitude]*best from 1-16}}, p_{\text{best from 1-16}}\}$	\mathcal{N} : study site latitude and best model from 1-16 effects with all interactions. p : same as model 17.

^a Model subscripts indicate study area (g), time (t , T), ecological province (prov) or ownership (owner) effects. Time effects were either year-specific (t) or linear (T).

territory for many years. This confounding could cause lack of independence, which tended to underestimate the standard errors. For this reason, mixed models (Rao 1997) were used to analyze these data under a maximum likelihood framework. This type of model had a number of advantages (Littel et al. 1996): 1) modeling could be placed in a maximum-likelihood framework; (2) models allowed for the correct inference (e.g., to sites or birds on sites rather than to separate outcomes/year) by appropriate adjustments of the standard errors, (3) models could be run as a “weighted”-type regression by structuring the error covariance matrix, and (4) models allowed for unbalanced designs (e.g., missing data).

Individual Study Areas

Preliminary plots of the data showed a strong biannual cyclic pattern to the number of young fledged with higher success rates in even years compared to odd years, which seemed to occur across all three age classes (Fig. 2). We called this effect the even/odd year effect. Preliminary plots also showed that the variation in the number fledged within a year was proportional to the mean, suggesting a Poisson distribution (Evans et al. 1993). However, examination of histograms for individual years within studies indicated that the data were not distributed as Poisson. Despite the integer nature of the data, the sample sizes were sufficiently large to justify normal distributional assumptions (see White and Bennetts 1996) as long as allowance was made for the dependence of the variation on the mean. Most (~ 80%) birds were seen on only one territory, based on an initial tabulation of the number of territories where each female bird was sighted. Consequently, we did not extract the separate bird from territory effects; bird effects were ignored and assumed to be incorporated with territory effects.

PROC MIXED (SAS Institute 1997) was used to fit various models for the mean number fledged for each study area. In these initial models, there was strong evidence of an even/odd year and age effect in most study areas (Table 4), but no evidence of a linear trend in the mean number of young fledged over time. There was no evidence of an interaction between female age and the even/odd year effect, and between female age and years for most study areas; these terms were not included in the models. Therefore, the final model for each study site included fixed effects of even/odd years and female age, and random effects of territory and year within each even/odd class. The final model also allowed for the variance of responses to be dependent on both female age and even/odd years. Therefore, the SAS code for the basic model fit for each study area was:

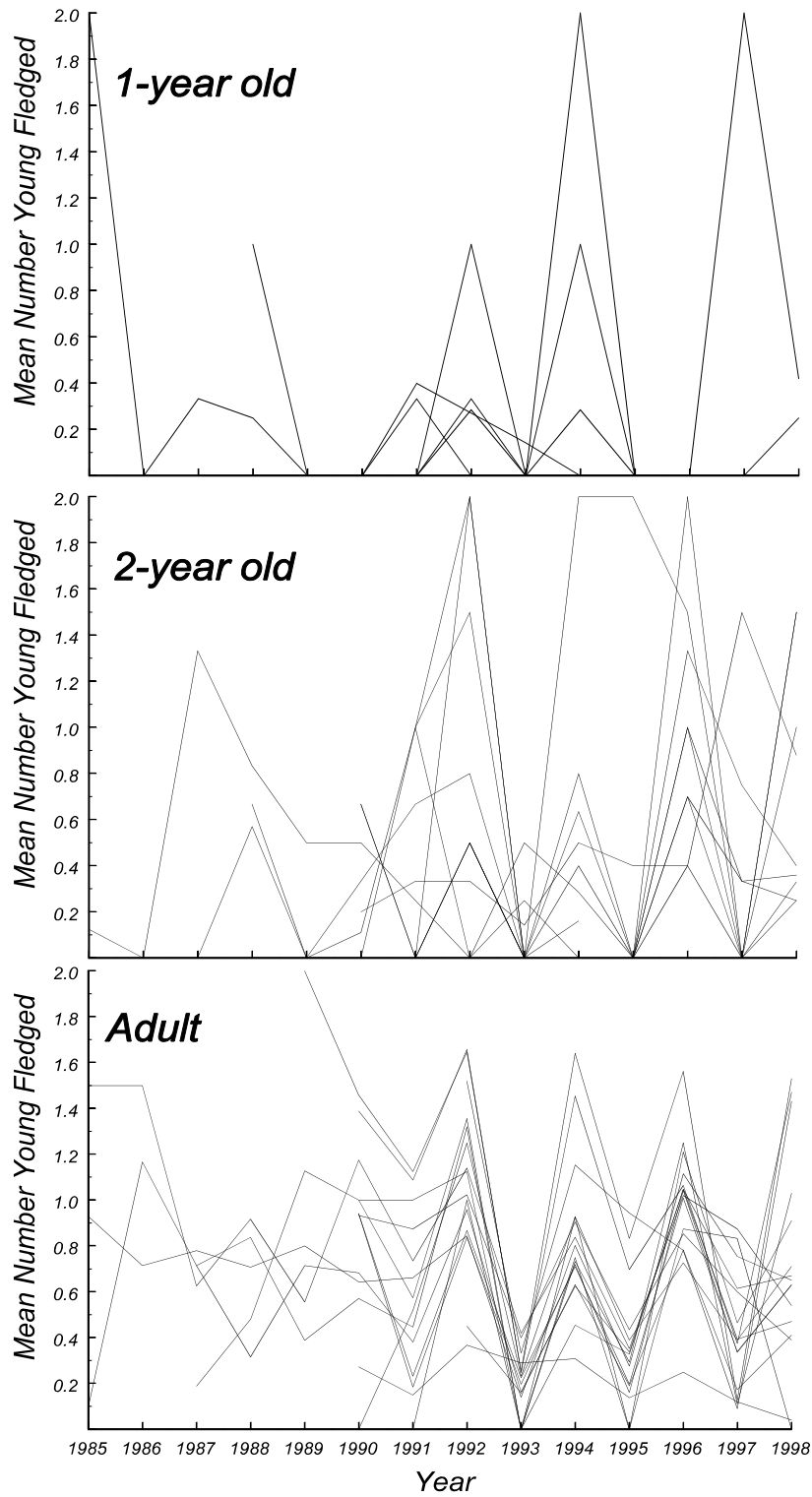


FIGURE 2. Preliminary plots of mean number of young fledged per female Northern Spotted Owl on 15 study areas.

MODEL FLEDGE = FAGE EVENODD FAGE*EVENODD /DDFM=SATTERTH;
RANDOM LOCATION YEAR ;
REPEATED / LOCAL=EXP(FAGE EVENODD);

where FLEDGE is the number of young fledged per female each year, FAGE is female age-class, EVENODD is the even/odd year effect, LOCATION is owl territory, and YEAR is the year. To account for the proportional relationship between annual means and variances, a log-linear variance model (LOCAL=EXP in above SAS code) was used to properly structure the error covariance matrix (Littel et al. 1996:294). In this model, the mean number of young fledged depends upon the age of the bird and if it is an even or odd year. This model was used for all study areas except HUP and WSR. For the latter areas the model did not converge because of sparse data, so we used a simpler model in which the variance depended only upon the even/odd year effect.

TABLE 4. Tests of even-odd year effect (EVENODD) and female age effect (FAGE) in preliminary mixed model analysis of variance of fecundity for female Northern Spotted Owls on 16 study areas.

Study Area	Pr > F under H ₀ of no effect:	
	EVENODD	FAGE
AST	0.237	0.974
CAS	0.009	0.279
CLE	0.014	0.000
COA	0.000	0.003
EEU	0.387	0.291
ELC	0.000	0.001
HJA	0.031	0.002
HUP	0.017	0.318
KLA	0.029	0.001
NWC	0.216	0.000
OLY	0.019	0.136
RAI	0.000	0.007
SIM	0.127	0.000
TYE	0.027	0.000
WEN	0.004	0.000
WSR	0.045	0.025

Meta-analysis across Study Areas

We performed three separate meta-analyses on the fecundity data: one using all 15 study areas, one using only the eight monitoring areas, and one using 13 study areas that could be assigned to either a strict or relaxed protocol category to examine differences in protocols for determining number of fledged young in the field. The latter analysis stemmed from concerns that not every study followed the same protocols for collecting fecundity data. Two basic protocols had been used, a *strict protocol* where four mice were fed to owls on each of two visits (see Franklin et al. 1996), and a *relaxed protocol* where fewer than four mice were fed on a visit and/or only one visit was made to a site within a given year. We recognize that protocol and

study area were confounded, and that this confounding could not be removed. In these analyses, only adult females were used because of sparse data in the 1- and 2-year old age-classes. In addition, we examined fecundity in relationship to the ecological province and ownership categories used in conducting the meta-analysis of trends in female survival.

Again, mixed models were used to perform the meta-analyses in fecundity. Because the analysis was restricted to adult females whose mean fledging rate is relatively constant, we did not allow for differential variances in the number fledged. We also ignored variation attributable to territories because it was small relative to the residual variation. The key feature of this analysis is the proper identification of the experimental unit - conceptually, birds are 'subsamples' within year-study area combinations and should not be treated as the final experimental unit. Thus, individual females were not the experimental unit. A particular province*year treatment combination was applied to each study area, and then birds within this study area were measured. Therefore, the experimental units were study areas(province*year), which we used as a random effect in the mixed models. This was not strictly correct, but the 'error' introduced by this approximation was expected to be small.

We used model selection procedures to evaluate the effects of province, ownership, and time on fecundity. We used AIC for model selection, with ΔAIC , and Akaike weights (w_i) as additional criteria for evaluating models. We did not use the small sample bias-corrected version of AIC (AICc) because sample sizes were large. In addition, we were unable to correct for lack of fit using $\hat{\sigma}^2$ as we did with the analysis of survival probabilities. Here, we relied on the robustness of these parametric methods to non-normality and the ability to account for heteroscedasticity through modeling of the error matrix.

RATES OF POPULATION CHANGE

A general question of interest here was whether populations were increasing ($\lambda > 1$), stationary ($\lambda = 1$), or decreasing ($\lambda < 1$) and at what annual rate. Annual rates of population change (λ) were estimated in two ways. First, λ was estimated for each study area from estimates of age-specific survival and fecundity using a Leslie projection matrix (Lande 1988, Noon and Biles 1990, Noon and Sauer 1992). Estimates from this method were referred to as λ_{PM} (where PM stood for “projection matrix”) and represented average estimates of the rate of population change across time. Second, λ was estimated directly from capture history data (following Pradel 1996) selected from portions of certain study areas that met specified criteria (see below). Estimates from this method were referred to as λ_{RJS} (where RJS referred to “reparameterized Jolly-Seber”) and represented estimates based on apparent survival and

recruitment which could be time-specific, depending on which model was most parsimonious. In terms of the overall analyses presented here, estimation of \mathcal{S}_{RJS} was considered exploratory because this methodology had not been previously applied to Northern Spotted Owl data and had seen little use since its development. These approaches are explained in more detail below.

Estimation of \mathcal{S}_{PM} for Individual Study Areas

Annual rates of population change (\mathcal{S}_{PM}) were estimated for each study area using a formulation of the Leslie projection matrix (Leslie 1945, Caswell 1989, McDonald and Caswell 1993). Estimates of \mathcal{S}_{PM} represented the asymptotic rate of population change that would occur if the average survival and fecundity rates estimated over the study period occurred year after year. We viewed \mathcal{S}_{PM} as an estimate of the average rate of population change over the period from which the survival and fecundity estimates were obtained. We used the estimates (and their standard errors) for age-specific fecundity from the mixed models and calculated mean estimates for age-specific survival as follows. For survival models that had a linear time trend (T) on N , we used the midpoint of the predicted estimates and its standard error. For models that had a variable time structure (t) on N , we used a random-effects model (Burnham, in prep.) to estimate $\bar{\phi}$ and $\text{se}(\bar{\phi})$. For models with a pseudo-threshold ($\ln T$) or quadratic (TT) structure on N , we averaged the annual predicted estimates and used the standard error from the closest predicted estimate.

The estimate of \mathcal{S}_{PM} is a measure of the average direction ($\mathcal{S}_{\text{PM}} = 1$ indicating a stationary population, $\mathcal{S}_{\text{PM}} < 1$ a declining population and $\mathcal{S}_{\text{PM}} > 1$ an increasing population) and magnitude ($\mathcal{S}_{\text{PM}} - 1$) of the change in population over the time period when the population was sampled. We used only females to estimate \mathcal{S}_{PM} . We used two matrix models to estimate \mathcal{S}_{PM} from the Northern Spotted Owl data for the individual study areas. Choice of the matrix model depended on the structure of the best model for age-specific survival from the individual study areas. In all cases, fecundity was estimated for three age-classes (1-year old, 2-year old, and adult). If the best model for N supported only two age-classes, juveniles and non-juveniles, then a three age-class matrix was used:

$$\begin{bmatrix} \hat{\phi}_0 \hat{b}_1 & \hat{\phi}_{1+} \hat{b}_2 & \hat{\phi}_{1+} \hat{b}_3 \\ \hat{\phi}_0 & 0 & 0 \\ 0 & \hat{\phi}_{1+} & \hat{\phi}_{1+} \end{bmatrix}$$

where subscript “0” indicated parameter estimates for juveniles, subscript “1+” indicated parameter estimates for non-juveniles, and subscripts “1”, “2”, and “3” indicated parameter

estimates for 1-year old, 2-year old, and adult age-classes, respectively. Where all non-juvenile age-classes were supported, we used the full matrix model that included all four age-classes:

$$\begin{bmatrix} \phi_0 \hat{b}_1 & \phi_1 \hat{b}_2 & \phi_2 \hat{b}_3 & \phi_3 \hat{b}_3 \\ \phi_0 & 0 & 0 & 0 \\ 0 & \phi_1 & 0 & 0 \\ 0 & 0 & \phi_2 & \phi_3 \end{bmatrix}$$

Both matrix models assumed a birth-pulse population, a post-breeding “census”, and a time interval of one year (Noon and Sauer 1992). Estimates of \mathcal{S}_{PM} were computed from the characteristic polynomial of the matrix models. Estimates of $\hat{se}(\lambda_{PM})$ were computed using the delta method (Alvarez-Buylla and Slatkin 1994) based on estimated sampling variances of the age-specific survival and fecundity estimates and their sampling correlations.

Estimation of \mathcal{S}_{RJS} for Individual Study Areas

Pradel (1996) introduced a reparameterization of the Jolly-Seber model permitting estimation of \mathcal{S}_t , the finite rate of population increase (defined by N_{t+1}/N_t where N_t represents population size at time t) in addition to local apparent survival (\mathcal{M}) and recapture probability (p). This parameterization was recently encoded in program MARK and used with the Northern Spotted Owl capture-recapture data. We referred to this parameterization that incorporated \mathcal{S} as \mathcal{S}_{RJS} . In addition to the ability to obtain time-specific estimates of \mathcal{S}_{RJS} , the models implemented in MARK also allowed for constraints, such as linear or non-linear time parameterizations of \mathcal{S}_{RJS} .

The estimates of \mathcal{S}_{RJS} reflected changes in population size resulting from reproduction, mortality, and movement. The data used in the analyses included only territorial individuals of mixed age-classes (e.g., no differentiation between adults and 1-, or 2-year olds). This approach did not require separation of losses from the population due to mortality and emigration, or of gains from reproduction and immigration. Thus, the estimates of \mathcal{S}_{RJS} from any particular capture-recapture data set should correspond to changes in the territorial population on the specific sampled portions of the study area. If only territorial birds were exposed to sampling efforts, $\hat{\lambda}_{RJS}$ resulting from the analysis reflected the rate of change in abundance of territorial birds. Gains in the territorial population could result from recruitment of floaters (birds that were perhaps present on the study area but not previously territorial and, hence, not exposed to previous capture efforts), and recruitment from immigration of birds outside the study area.

TABLE 5. Descriptions of portions of study areas used to estimate \mathcal{S}_{RJS} for female Northern Spotted Owls. Study area type was either density study area (DSA) or collection of sites (CSA). Size for DSA types is area of the study area and for CSA types is the number of owl sites.

Study area	Type	Years	Size
CAS	CSA	1991 - 1998	44 sites
CLE	CSA	1992 -1998	53 sites
COA	CSA	1992 - 1998	147 sites
ELL	DSA	1992 - 1998	376 km ²
HJA	DSA	1988 - 1998	317 km ²
HUP	DSA	1992 - 1998	356 km ²
KLA	CSA	1991 - 1998	95 sites
NWC	DSA	1985 - 1998	292 km ²
OLY	DSA	1989 - 1990	1,815 km ²
RAI	CSA	1993 - 1998	22 sites
SIM	DSA	1992 - 1998	1,265 km ²
TYE	DSA	1990 - 1998	1,025 km ²
WSR	CSA	1993 - 1998	47 sites

With respect to study areas, we distinguished two primary types of study design (Table 5, Fig. 3). Density Study Areas (DSA's) were probably most appropriate for unbiased estimation of λ_{RJS} because they were well-defined by boundaries, and the entire areas were sampled each year. All owls in these areas were considered exposed to sampling efforts each year. Thus, interpretation of $\hat{\lambda}_{\text{RJS}}$ as applying to changes in numbers of territorial owls on DSA's seemed reasonable. The other type of study area design did not involve a single, contiguous area, but instead included discrete, territorial sites defined at the beginning of the study. These sites were identified and surveyed during the initial year of study and revisited during each subsequent year. In some

studies, these sites were selected on the basis of occupancy in the first year of the study, such that all study sites were initially occupied. In most situations, the set of sites was selected based on historical occupancy records, such that the sample included occupied and unoccupied sites in the first year of study. The critical aspect of the sampling in both situations was that all sites in the initial sample of sites were visited during each subsequent year of the study, regardless of recent occupancy status (e.g., even if no owls were detected on sites for several consecutive years).

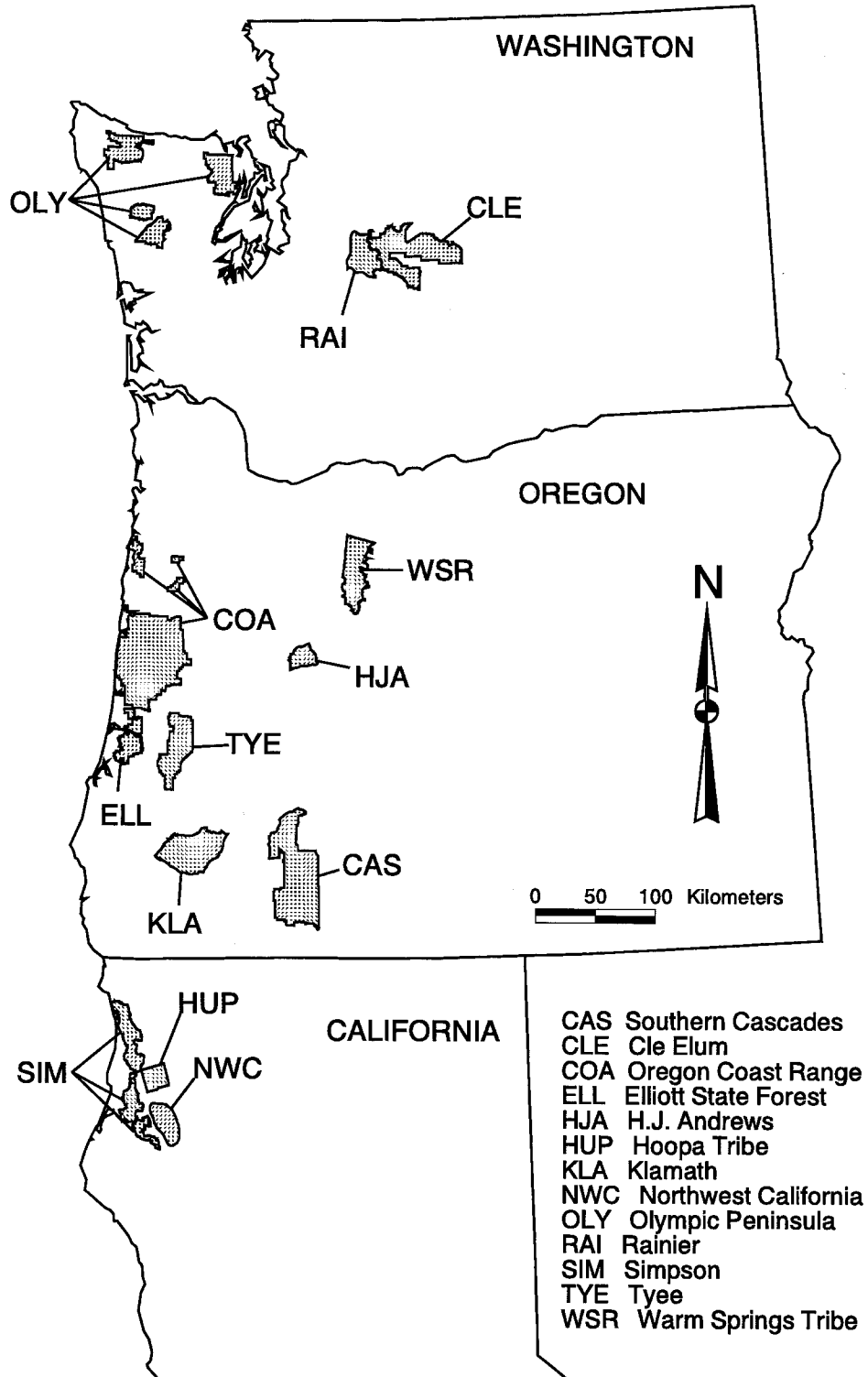


FIGURE 3. Map showing the location of the 12 portions of Northern Spotted Owl demographic study areas used to estimate δ_{RJS} from capture-recapture data.

In the case of discrete study sites, the interpretation of $\hat{\lambda}_{\text{RJS}}$ is similar to that for the DSA's; changes in the number of owls on the sampled area(s) were being estimated. However, in the case of discrete sites, it may also be reasonable to consider the estimates in terms of patch-occupancy models. In this case, $\hat{\lambda}_{\text{RJS}}$ should estimate a quantity closely related to the rate of change in the proportion of occupied patches. Because some sets of study sites were all occupied in year 1 and others were not (were selected on the basis of historical records), it would likely be useful to interpret each estimate, $\hat{\lambda}_{\text{RJS}}$, in the context of the initial proportion of known occupancy (the fraction of the set of sites that is occupied initially). For example, if all sites are known to be occupied in the first year of a study, then the proportion of occupied sites cannot increase. Our analysis of $\hat{\lambda}_{\text{RJS}}$ included data from 13 study areas including seven DSAs (ELL, HJA, HUP, NWC, OLY, SIM, TYE) and six sets of selected spotted owl sites (CAS, CLE, COA, KLA, RAI, WSR) (Table 5, Fig. 3). Regardless of study area design, we used five *a priori* models for estimating \mathcal{G}_{RJS} , and for investigating sources of variation over time in this parameter:

- 1) $\{\mathcal{G}_{\text{RJS}}(\cdot)\}$, no trend in \mathcal{G}_{RJS} over time;
- 2) $\{\mathcal{G}_{\text{RJS}}(T)\}$, linear trend in \mathcal{G}_{RJS} over time;
- 3) $\{\mathcal{G}_{\text{RJS}}(TT)\}$, quadratic trend in \mathcal{G}_{RJS} over time;
- 4) $\{\mathcal{G}_{\text{RJS}}(\ln T)\}$, pseudo-threshold trend in \mathcal{G}_{RJS} over time; and
- 5) $\{\mathcal{G}_{\text{RJS}}(t)\}$, varying annual estimates of \mathcal{G}_{RJS} over time.

Recapture probabilities for each study area were structured according to the best capture-recapture model for non-juvenile survival. These structures were used across the suite of models estimating \mathcal{G}_{RJS} for each study area. Goodness-of-fit was evaluated using the parametric bootstrap procedures described for survival models. Goodness-of-fit was performed on the $\{\mathcal{N}_i, p_i\}$ model for each data set.

Although the reparameterized model is conceptually sound, there are legitimate concerns about its applicability to spotted owl data. Specifically, certain underlying model assumptions are likely to be violated so we conducted some initial investigations into possible consequences of violating underlying model assumptions when estimating \mathcal{G}_i (Appendix D). We considered three specific kinds of assumption violations: expansion of study area over time, permanent trap response in capture probability, and heterogeneous capture probabilities.

TABLE 6. Estimates of overdispersion (\hat{c}) and goodness-of-fit (percentile) for 16 Northern Spotted Owl capture-recapture data sets using four age-classes. Mean deviances and percentiles are based on 500 bootstrap resamplings under the global model $\{N_{a(s(t)}, p_{a(s(t))}\}$ fitted to the data assuming $c = 1$.

Study Area	Observed Deviance	Mean Deviance	\hat{c}	Percentile ^a
AST	57.384	40.267	1.425	0.009
CAS	285.076	205.791	1.385	0.000
CLE	379.894	301.373	1.261	0.000
COA	630.639	506.864	1.244	0.000
ELC	672.164	538.324	1.249	0.000
EEU	248.019	214.332	1.157	0.067
HJA	1063.817	918.663	1.158	0.005
HUP	150.793	112.962	1.335	0.003
KLA	1050.046	918.422	1.143	0.007
NWC	983.400	839.028	1.172	0.001
OLY	1140.840	911.276	1.252	0.000
RAI	66.218	53.492	1.238	0.077
SIM	994.447	841.364	1.182	0.000
TYE	855.817	752.326	1.138	0.009
WEN	558.501	482.317	1.158	0.009
WSR	156.760	111.610	1.405	0.001

^asame as a P -value for H_0 : model fits the data

RESULTS

SURVIVAL ESTIMATES

Individual Study Areas

Most of the age-specific capture-recapture data for the individual study areas exhibited lack of fit to the global Cormack-Jolly-Seber model (Table 6). However, estimates of overdispersion (\hat{c}) were not large (range = 1.15 - 1.43; Table 6). We used the estimates of \hat{c} as a quasi-likelihood inflation factor to adjust model selection procedures and variance estimates in

TABLE 7. Estimates of average apparent survival (\hat{N}) for four age-classes of Northern Spotted Owls on 16 study areas. Descriptions of models are in Table 2.

Study area	Best Model		Juvenile		1-year old		2-year old		Adult	
	\hat{N} structure	p structure	$\hat{\phi}_0$	$\hat{se}(\hat{\phi}_0)$	$\hat{\phi}_1$	$\hat{se}(\hat{\phi}_1)$	$\hat{\phi}_2$	$\hat{se}(\hat{\phi}_2)$	$\hat{\phi}_3$	$\hat{se}(\hat{\phi}_3)$
AST	$\hat{N}_{[J,NJ]+T}$	$p_{[a4'+s],[NJ+s+T]}$	0.378	0.348	0.842	0.041	0.842	0.041	0.842	0.041
CAS	$\hat{N}_{J,[[S1,S2,A]+t]}$	$p_{a4',NJ}$	0.284	0.198	0.382	0.257	0.576	0.113	0.816	0.017
CLE	$\hat{N}_{[J,NJ]+t}$	$p_{[a4'+s],NJ}$	0.195	0.028	0.839	0.015	0.839	0.015	0.839	0.015
COA ^a	$\hat{N}_{J,[NJ+T]}$	$p_{[a4'+s],[NJ+T]}$	0.366	0.042	0.887	0.010	0.887	0.010	0.887	0.010
EEU	$\hat{N}_{J,[[S1,S2,A]+t]}$	$p_{[a4'+s],[NJ+s+T]}$	0.159	0.149	0.297	0.124	0.721	0.258	0.823	0.020
ELC	$\hat{N}_{J,[NJ+T]}$	$p_{[a4'+s],[NJ+T]}$	0.394	0.040	0.882	0.009	0.882	0.009	0.882	0.009
HJA	$\hat{N}_{[J,S1,S2,A]+t}$	$p_{a4',[NJ+t]}$	0.305	0.063	0.535	0.085	0.956	0.041	0.871	0.010
HUP	$\hat{N}_{J,[NJ+T]}$	$p_{[a4'+s],[NJ+s+effort]}$	0.366	0.131	0.820	0.025	0.820	0.025	0.820	0.025
KLA	$\hat{N}_{J,[NJ+lnT]}$	$p_{a4',NJ}$	0.364	0.036	0.833	0.016	0.833	0.016	0.833	0.016
NWC	$\hat{N}_{[J,NJ]+lnT}$	$p_{a4',[NJ+cap\ tech+wet\ yrs]}$	0.295	0.031	0.860	0.009	0.860	0.009	0.860	0.009
OLY	$\hat{N}_{[J,S1,S2,A]+t}$	$p_{a4',[NJ+fecundity]}$	0.252	0.060	0.587	0.102	0.708	0.072	0.826	0.012
RAI	$\hat{N}_{J,[NJ+ln(T)]}$	$p_{J,[NJ+t]}$	n.e. ^b		0.895	0.031	0.895	0.031	0.895	0.031
SIM	$\hat{N}_{[J,NJ]+T}$	$p_{[a4'+s],[NJ+s]}$	0.365	0.029	0.859	0.008	0.859	0.008	0.859	0.008
TYE	$\hat{N}_{J,[NJ+TT]}$	$p_{[a4'+s],[NJ+s+T]}$	0.446	0.036	0.869	0.014	0.869	0.014	0.869	0.014
WEN	$\hat{N}_{[J,S1,S2,A]+t}$	$p_{[a4'+s],[NJ+s]}$	0.143	0.030	0.697	0.124	0.646	0.072	0.836	0.012
WSR	$\hat{N}_{J,[NJ+ln(T)]}$	$p_{J,NJ}$	0.064	0.029	0.843	0.022	0.843	0.022	0.843	0.022

^aThis study was a subset of ELC

^bNot estimable

the subsequent capture-recapture analyses. In this way, we were able to adjust for initial, minor lack of fit.

Best models for nine of the 15 studies (not including COA) had either linear or non-linear trends in apparent survival of non-juveniles (5 linear, 3 pseudo-threshold and 1 quadratic; Table 7). The trends exhibited by COA and ELC were considered a single study because COA was a subset of ELC. In the nine studies with linear, pseudo-threshold, or quadratic time trends in non-juvenile survival, four of the trends had positive slopes (ELC, KLA, RAI, WSR), four had negative slopes (AST, HUP, NWC, SIM) and one (TYE) had a negative quadratic trend (Table 8). However, trends in non-juvenile survival were supported by only four of the studies (ELC, HUP, NWC, and TYE) based on coefficients of sampling variation and the degree to which 95% confidence intervals included zero (Table 8). Two of these four studies exhibited negative trends

TABLE 8. Estimates of slope parameters ($\hat{\beta}_i$) and their standard errors ($\text{se}(\hat{\beta}_i)$) for individual study areas where models indicated linear, pseudo-threshold, or quadratic trends in non-juvenile annual survival probability. Slopes are in terms of $\text{logit}(M)$.

Study Area	Trend ^a	$\hat{\beta}_i$	$\text{se}(\hat{\beta}_i)$	CV ^b	95% confidence intervals
AST	<i>T</i>	-0.0823	0.2314	2.811	-0.5359, 0.3713
COA	<i>T</i>	0.1367	0.0466	0.341	0.0454, 0.2281
ELC	<i>T</i>	0.1060	0.0438	0.413	0.0201, 0.1919
HUP	<i>T</i>	-0.1966	0.1009	0.513	-0.3944, 0.0013
KLA	$\ln T$	0.1997	0.1841	0.922	-0.1613, 0.5606
NWC	$\ln T$	-0.2532	0.1101	0.435	-0.4469, -0.0374
RAI	<i>T</i>	0.2293	0.8295	3.618	-1.3966, 1.8551
SIM	<i>T</i>	-0.0244	0.0279	1.143	-0.0790, 0.0302
TYE ^c	<i>TT</i>	-0.2971	0.1392	0.469	-0.5699, -0.0243
		0.0169	0.0084	0.497	0.0004, 0.0333
WSR	$\ln T$	0.2887	0.2973	1.030	-0.2941, 0.8715

^a*T* = linear trend over time, $\ln T$ = psuedo-threshold trend over time, and *TT* = quadratic trend over time.

^bCoefficient of sampling variation (CV) computed as $\text{se}(\hat{\beta}_i)/|\hat{\beta}_i|$.

^cFirst $\hat{\beta}_i$ is for first term in quadratic, second $\hat{\beta}_i$ is for second term in quadratic.

(NWC and HUP), one (ELC) a positive trend, and one (TYE) with an initial negative trend that then became positive (i.e., a quadratic relationship; Fig. 4). The three study areas in California (HUP, SIM, NWC) all had negative time trends in non-juvenile apparent survival (Table 8, Fig. 4).

Most of the best models did not support linear time trends in juvenile apparent survival. Exceptions were AST, NWC, and SIM (Table 7) where a negative time trend in apparent survival for juveniles had the same slope as non-juveniles (Tables 7 and 8). However, there was evidence only for NWC that the slope differed from zero, based on 95% confidence intervals (Table 8). Models for five study areas (CAS, EEU, HJA, OLY, and WEN) supported separation

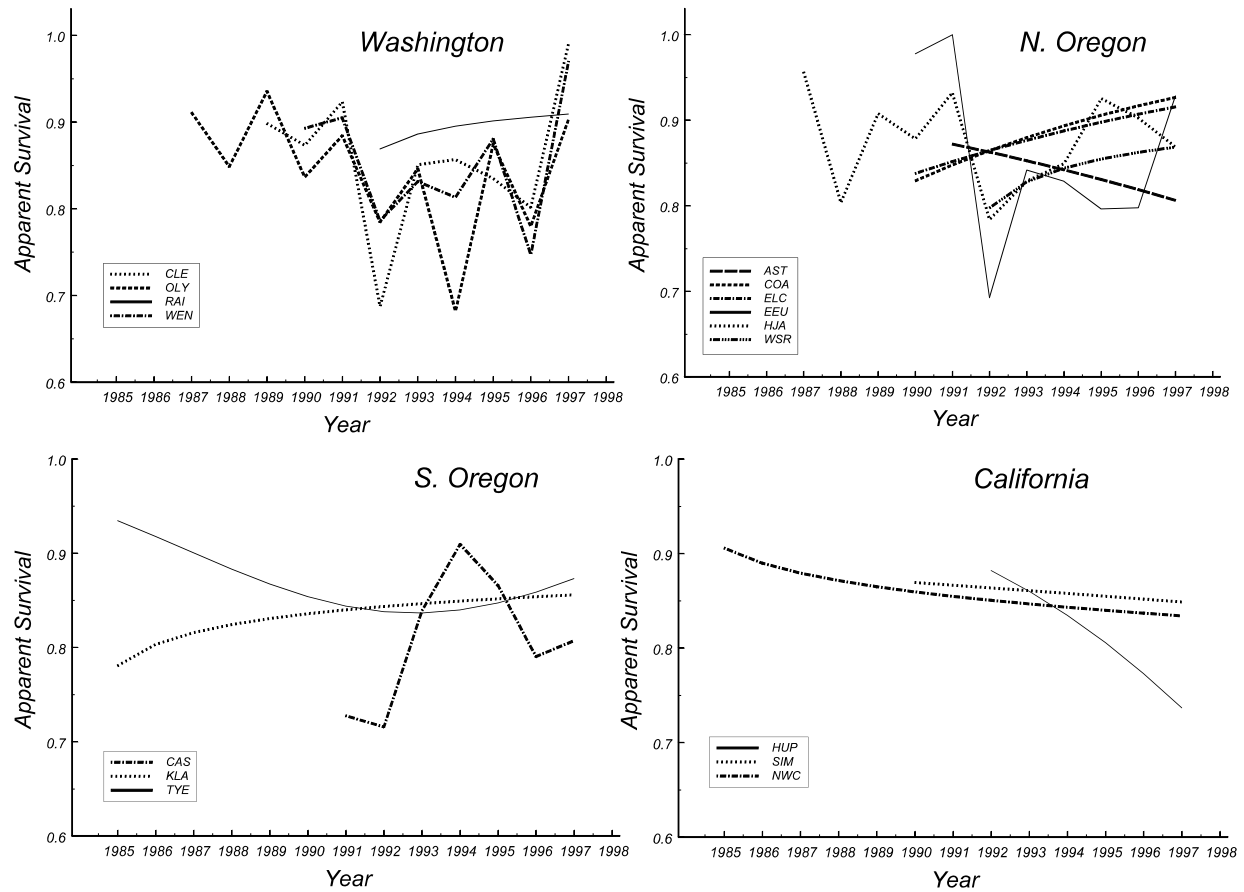


FIGURE 4. Trends in non-juvenile apparent survival for Northern Spotted Owls on 15 study areas in Washington, Oregon and California. Standard errors for estimates not shown (see Tables 7 and 8). Estimates are from best selected models.

of non-juvenile age-classes into 1-year, 2-year, and >3-year old classes. In all cases, these models varied by time with all three age-classes having parallel time structure (on a logit scale) within each study area (the “+ t ” models in Table 7). Mean estimates of apparent survival across study areas increased with age from 0.281 for juveniles to 0.850 for adults (Table 9). Survival probabilities for juveniles exhibited the most spatial variation across study areas while those of adults exhibited the least (see CV_{process} in Table 9).

Based on the radiotelemetry data from the TYE, OLY and CLE study areas, we estimated juvenile emigration rates (\hat{E}) ranging from 0.2954 to 0.5789 (Table 10). These estimates of E were relatively precise with CVs ranging from 0.151 to 0.196. The variation in estimates of E were apparently a function of differences in study area size, configuration and proximity to other study areas. We adjusted estimates of N_0 by \hat{E} to obtain the following estimates of S_0 : 0.5977 ($\hat{se}(\hat{S}_0) =$

TABLE 9. Estimates of mean apparent survival ($\bar{\phi}$) and spatial process variation ($\sigma_{spatial}^2$) for four age-classes of Northern Spotted Owls across 15 study areas. The COA study area was not included because it was used herein as a subset of the ELC study area.

Age-class	$\bar{\phi}$	$\hat{se}(\bar{\phi})$	$\hat{\sigma}_{spatial}^2$	95% CI for $\hat{\sigma}_{spatial}^2$	CV _{process} ^a
Juvenile	0.281	0.032	0.0095	0.0044, 0.0277	0.348
1-year old	0.778	0.042	0.0222	0.0071, 0.0751	0.192
2-year old	0.840	0.019	0.0042	0.0006, 0.0184	0.077
Adult	0.850	0.005	0.0003	0.0006, 0.0011	0.019

^aCoefficient of process variation computed as $\hat{\sigma}_{spatial}^2 / \bar{\phi}$

0.2149) for OLY; 0.6323 ($\hat{se}(\hat{S}_0) = 0.0650$) for TYE; and 0.3664 ($\hat{se}(\hat{S}_0) = 0.0816$) for CLE. These estimates of S_0 represented increases of 137.2%, 41.8% and 87.9% above the estimates of apparent survival of juveniles for the OLY, TYE and CLE study areas, respectively.

Meta-analysis of Adult Females

We examined trends in annual apparent survival of adult females in two meta-analyses: one with 15 study areas and one with the 8 monitoring areas. Estimates of over-dispersion (\hat{c}) were similar for both data sets ($\hat{c} = 1.194$ and 1.183, respectively) and were used to adjust model selection procedures and variance estimates in the subsequent capture-recapture analyses.

The best model from the meta-analysis of the 15 study areas was $\{N_t, p_{g*T}\}$ that indicated no study area effects on N but a variable time (t) effect (Table 11, Fig. 5). Two models, $N_{latitude+t}, p_{g*T}$ and $N_{ownership+t}, p_{g*T}$, were closely competitive to the selected model (Table 11) suggesting some effect due to latitude and land ownership (Table 11). However, none of these models explained a "significant" amount of the variation. Based on analysis of deviance (Skalski et al. 1993), neither latitude ($F_{1,13} = 1.2743$, $P = 0.2794$) or ownership ($F_{2,12} = 0.9953$, $P = 0.3982$) covariates were significant. Only because these covariates had a small increment in number of parameters over N_t did they appear competitive with the N_t model in the QAICc ranking. Therefore, the latitude and ownership covariates did not explain an important amount of the group variation. In addition, there was no evidence of linear, pseudo-threshold, or quadratic

TABLE 10. Estimates of emigration (E) from three study areas based on radio-marked juvenile Northern Spotted Owls.

Study area	Year	n_{en}	n	\hat{E}	$\hat{se}(\hat{E})$
TYE	1991	2	26	-	-
TYE	1992	11	31	-	-
TYE	1993	5	13	-	-
TYE	1994	13	35	-	-
TYE	All years	31	105	0.2954	0.0445
OLY	1991	8	11	-	-
OLY	1992	3	8	-	-
OLY	All years	11	19	0.5789	0.1133
CLE	1991	7	12	-	-
CLE	1992	3	4	-	-
CLE	1995	4	14	-	-
CLE	All years	14	30	0.4667	0.0911
All studies	All years	56	154	0.3636	0.0388

trends in N (Table 11). Based on Akaike weights, the best model $\{N_t, p_{g^*T}\}$ was almost 9 times as likely as the closest model with a quadratic structure on $N\{N_{TT}, p_{g^*T}\}$.

The best model from the meta-analysis of eight monitoring areas $\{N_{g+t}, p_{g^*T}\}$ was identical with the best model produced by the analysis of all 15 areas, except that it also included a study area (g) effect on N (Table 12, Fig. 5). The second-ranked model $\{N_{g+t}, p_{g+T}\}$ had an identical structure on N , but had a slightly different structure in p . Province and

ownership effects were included in the third- and fourth-ranked models but the first-ranked model was 5-6 times as likely as these models based on the Akaike weights (Table 12). There was little evidence for linear, pseudo-threshold, or quadratic trends in N . The best model was 13 times as likely as the closest model containing a quadratic time effect on $N(\{N_{g+TT}, p_{g^*T}\}$ in Table 12).

FECUNDITY ESTIMATES

Individual Study Areas

Age-specific fecundity, averaged over even and odd years, was estimated only for known-aged, paired females. Precision of fecundity estimates was high for adult females where there was substantial sample size, but poorer for 1- or 2-year old females where data were sparse (Table 13). The variance components estimated for the random effects in the mixed models showed that the contribution to the overall variation from territory or year was small relative to the unexplained residual variation (Table 14). Fecundity of 1- and 2-year old females, averaged

across study Model selection criteria for a priori models used in the meta-analysis of apparent survival for adult female Northern Spotted Owls on 15 study areas in Washington, Oregon, and California from 1985 through 1998.

Model	QAICc	Δ	w_i^a	K^b
$N_{t, p_{g^*T}}$	8009.345	0.00	0.329	43
$N_{\text{latitude}+t, p_{g^*T}}$	8009.575	0.23	0.293	44
$N_{\text{ownership}+t, p_{g^*T}}$	8010.536	1.19	0.181	45
$N_{\text{province}+t, p_{g^*T}}$	8013.487	4.14	0.041	46
$N_{TT, p_{g^*T}}$	8013.715	4.37	0.037	33
$N_{\text{latitude}+TT, p_{g^*T}}$	8014.273	4.93	0.028	34
$N_{\text{province}+\text{ownership}+t, p_{g^*T}}$	8014.924	5.58	0.020	48
$N_{g+t, p_{g+T}}$	8015.267	5.92	0.017	43
$N_{\text{ownership}+TT, p_{g^*T}}$	8015.583	6.24	0.015	35
$N_{\text{province}+TT, p_{g^*T}}$	8017.389	8.04	0.006	36
$N_{g+t, p_{g^*T}}$	8017.658	8.31	0.005	57
$N_{\text{province}+\text{ownership}+TT, p_{g^*T}}$	8019.466	10.12	0.002	38
$N_G p_{g^*T}$	8019.488	10.14	0.002	31
$N_{\text{province}*\text{ownership}+t, p_{g^*T}}$	8022.821	13.48	0.000	54
$N_{g+TT, p_{g^*T}}$	8023.452	14.11	0.000	47
$N_{g+t, p_{g+t}}$	8024.643	15.30	0.000	53
$N_{g+T, p_{g+T}}$	8025.309	15.96	0.000	32
$N_{g+\ln T, p_{g^*T}}$	8028.173	18.83	0.000	45
$N_{\text{province}*\text{ownership}+TT, p_{g^*T}}$	8028.395	19.05	0.000	44
$N_{g+T, p_{g^*T}}$	8030.117	20.77	0.000	46
$N_{g^*T, p_{g^*T}}$	8031.684	22.34	0.000	55
$N_{g+T, p_{g+t}}$	8031.840	22.49	0.000	43
$N_{g^*T, p_{g+t}}$	8036.619	27.27	0.000	56
N_g, p_g	8045.373	36.03	0.000	30
$N_{g^*T, p_{g+T}}$	8058.709	49.36	0.000	43
$N_{g+T, p_{g^*t}}$	8081.644	72.30	0.000	126
$N_{g^*t, p_{g^*T}}$	8081.869	72.52	0.000	145
$N_{g^*T, p_{g^*t}}$	8082.567	73.22	0.000	136
$N_{g^*t, p_{g+T}}$	8083.035	73.69	0.000	136
$N_{g+t, p_{g^*t}}$	8109.763	100.42	0.000	152
$N_{g^*t, p_{g+t}}$	8117.334	107.99	0.000	155
$N_{g^*t, p_{g^*t}}$	8226.106	216.76	0.000	252

^aAkaike weights.

^bNumber of parameters.

TABLE 12. Model selection criteria for *a priori* models used in the meta-analysis of apparent survival of adult female Northern Spotted Owl survivals on eight monitoring areas in Washington, Oregon, and California from 1985 through 1998.

Model	QAICc	Δ	w_i^a	K^b
$\mathcal{N}_{g+t}, p_{g^*T}$	5374.002	0.00	0.391	36
$\mathcal{N}_{g+t}, p_{g+T}$	5374.954	0.95	0.243	29
$\mathcal{N}_{\text{province*ownership}+t}, p_{g^*T}$	5377.102	3.10	0.083	33
$\mathcal{N}_{\text{ownership}+t}, p_{g^*T}$	5377.603	3.60	0.065	30
\mathcal{N}_t, p_{g^*T}	5377.841	3.84	0.057	29
$\mathcal{N}_{\text{latitude}+t}, p_{g^*T}$	5378.429	4.43	0.043	30
$\mathcal{N}_{\text{province}+t}, p_{g^*T}$	5378.984	4.98	0.032	31
$\mathcal{N}_{\text{province+ownership}+t}, p_{g^*T}$	5379.028	5.03	0.032	32
$\mathcal{N}_{g+TT}, p_{g^*T}$	5379.172	5.17	0.029	26
$\mathcal{N}_{g+\ln(T)}, p_{g^*T}$	5381.651	7.65	0.009	25
$\mathcal{N}_{g+T}, p_{g^*T}$	5381.886	7.88	0.008	25
$\mathcal{N}_{g+T}, p_{g+T}$	5383.006	9.00	0.004	18
$\mathcal{N}_{g^*T}, p_{g+T}$	5384.666	10.66	0.002	25
$\mathcal{N}_{g^*T}, p_{g^*T}$	5385.448	11.45	0.001	32
$\mathcal{N}_{g+t}, p_{g+t}$	5386.168	12.17	0.001	39
\mathcal{N}_g, p_g	5397.046	23.04	0.000	16
$\mathcal{N}_{g^*T}, p_{g+t}$	5397.367	23.36	0.000	36
$\mathcal{N}_{g+T}, p_{g+t}$	5409.863	35.86	0.000	29
$\mathcal{N}_{g^*t}, p_{g^*T}$	5411.559	37.56	0.000	96
$\mathcal{N}_{g^*t}, p_{g+T}$	5416.982	42.98	0.000	91
$\mathcal{N}_{g^*t}, p_{g+t}$	5433.034	59.03	0.000	102
$\mathcal{N}_{g^*T}, p_{g^*t}$	5435.800	61.80	0.000	94
$\mathcal{N}_{g+t}, p_{g^*t}$	5442.283	68.28	0.000	102
$\mathcal{N}_{g+T}, p_{g^*t}$	5454.897	80.89	0.000	89
$\mathcal{N}_{g^*t}, p_{g^*t}$	5492.833	118.83	0.000	162

^aAkaike weights.

^bNumber of parameters.

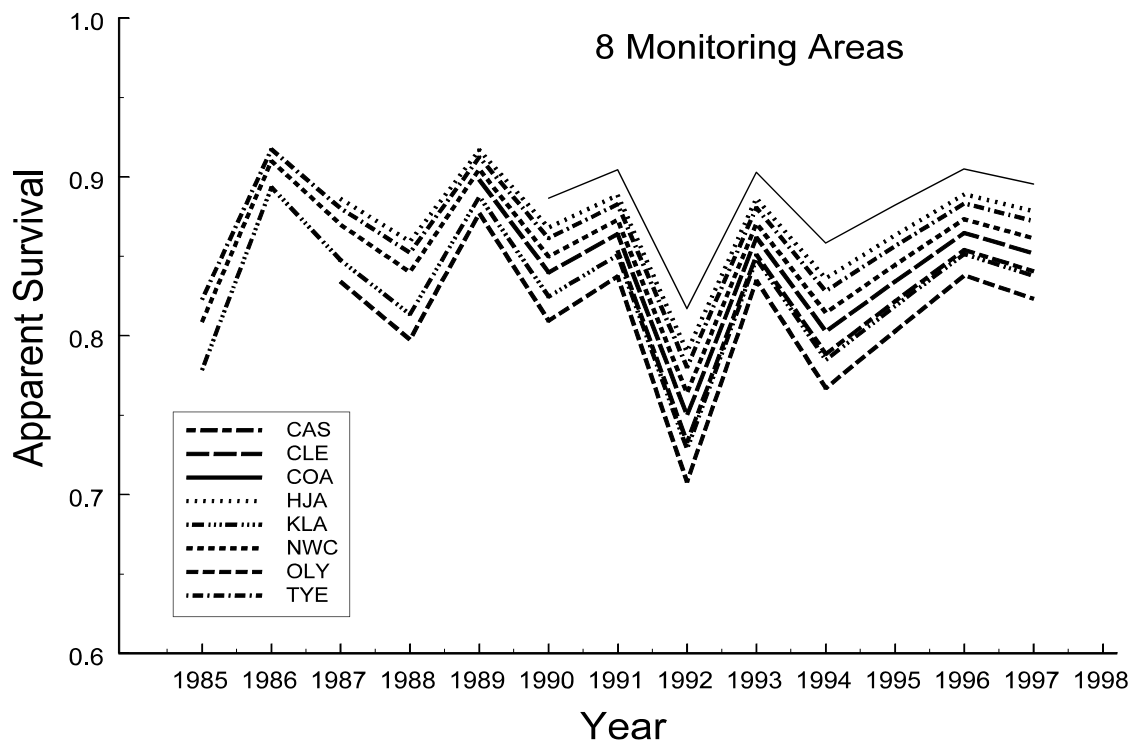
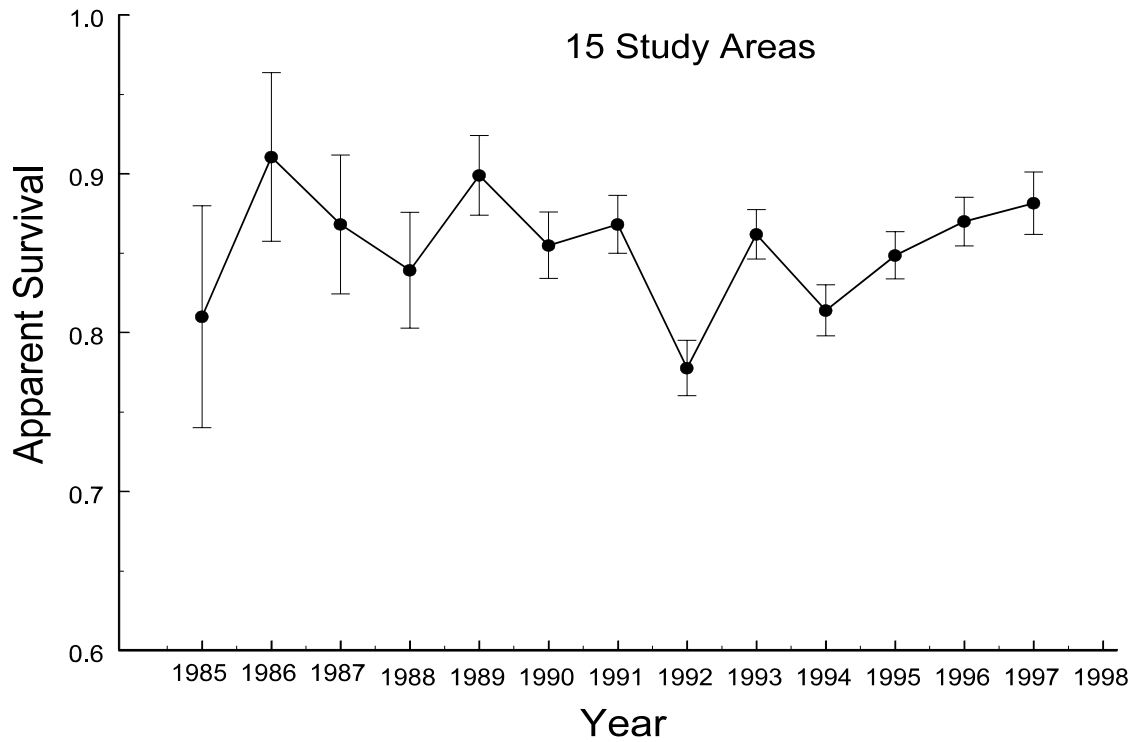


FIGURE 5. Estimates of apparent survival (\hat{N}) from best models for adult female Northern Spotted Owls from meta-analyses of 15 study areas and 8 monitoring areas. Error bars on graph for 15 study areas are \pm one standard error.

TABLE 14. Variance estimates for the random effects, LOCATION and YEAR in mixed model analysis of fecundity for Northern Spotted Owls on 16 study areas using mixed models that included effects of even-odd years, female age-class, year and site. Estimates are averaged across even-odd years.

Study area	LOCATION	1-year old	YEAR	Residual	2-year old	Adult			
Study area	n	\hat{b}_1	$se(\hat{b}_1)$	n	\hat{b}_2	$se(\hat{b}_2)$	n	\hat{b}_3	$se(\hat{b}_3)$
AST	0	0.049	0.125	0.460	0.231	0.3473	49	0.2239	0.0837
CAS	0	0.007	-	0.030	0.640	0.677	514	0.3209	0.0334
CAS	3	0.1593	0.0905	0.133	0.18	0.1701	514	0.3209	0.0334
CLE	0	0.076	-	0.133	0.614	0.823	306	0.5678	0.0638
CLE	19	0.1453	0.0883	0.015	0.24	0.553	306	0.5678	0.0638
COA	0	0.000	-	0.528	0.543	0.343	731	0.2583	0.0237
COA	9	0.0735	0.0407	0.226	0.32	0.0735	731	0.2583	0.0237
EEU	0	0.061	-	0.004	0.226	0.291	223	0.1029	0.0226
EEU	0	0.003	-	0.013	0.7	0.000 ^a	223	0.1029	0.0226
ELC	0	0.003	-	0.013	0.541	0.537	797	0.2629	0.0210
ELC	12	0.0304	0.0391	0.072	0.34	0.1167	797	0.2629	0.0210
HJA	0	0.027	-	0.072	0.541	0.639	659	0.2894	0.0410
HJA	13	0.0302	0.0870	0.002	0.24	0.0921	659	0.2894	0.0410
HUP	0	0.038	-	0.002	0.346	0.386	142	0.1717	0.0298
HUP	5	0.0908	0.1173	0.034	9	0.0855	142	0.1717	0.0298
KLA	0	0.000	-	0.671	0.671	0.705	507	0.3939	0.0300
KLA	30	0.1298	0.0502	0.041	59	0.2725	507	0.3939	0.0300
NWC	0	0.029	-	0.638	0.638	0.708	703	0.3487	0.0324
NWC	47	0.0578	0.0441	0.051	58	0.2183	703	0.3487	0.0324
OLY	0	0.014	-	0.551	0.551	0.683	656	0.3440	0.0525
OLY	4	0.1499	0.1634	0.522	10	0.1656	656	0.3440	0.0525
RAI	0	0.000	-	0.522	0.522	0.522	118	0.2912	0.0325
RAI	5	0.0272	0.0807	0.035	5	0.000 ^a	118	0.2912	0.0325
SIM	0	0.041	-	0.587	0.587	0.663	752	0.3490	0.0338
SIM	33	0.1100	0.0645	0.042	73	0.1183	752	0.3490	0.0338
TYE	0	0.023	-	0.550	0.550	0.615	673	0.2985	0.0314
TYE	41	0.0673	0.0395	0.061	58	0.1560	673	0.2985	0.0314
WEN	0	0.061	-	0.644	0.644	0.767	509	0.4921	0.0458
WEN	13	0.1137	0.0740	0.061	39	0.2865	509	0.4921	0.0458
WSR	0	0.000	-	0.637	0.637	0.759	227	0.4195	0.0719
WSR	5	0.2871	0.1760	0.122	12	0.0977	227	0.4195	0.0719

^aEstimates were slightly below zero and were truncated to zero for estimating δ_{PM} .

^aEstimates were slightly below zero and were truncated to zero for estimating δ_{PM} .

Fecundity estimates for 2-year old females exhibited greater variation across study areas than either 1-year old or adult females (see $CV_{process}$ estimates in Table 15).

Meta-analysis of Fecundity

Interactions between years, even-odd years and geographic province were not significant in preliminary models, and were excluded from further consideration. Similarly, the contribution of territory was less than 3% of residual variation; territory was, therefore, not included as a random effect in the final analyses.

In the meta-analysis of 15 study areas, the best model was $\{b_{prov+eo}\}$, which indicated that fecundity varied by even-odd years and ecological province (Tables 16 and 17). The East Slope province had the highest fecundity, followed by Mixed Conifer, Redwood, and Douglas-fir

TABLE 15. Estimates of mean fecundity (\bar{b}) and spatial process variation ($\sigma^2_{spatial}$) for Northern Spotted Owls across 15 study areas. The COA study area was not included for this analysis because it was a subset of the ELC study area.

Age-class	\bar{b}	$se(\bar{b})$	$\hat{\sigma}^2_{spatial}$	95% CI for $\hat{\sigma}^2_{spatial}$	$CV_{process}^a$
1-year old	0.078	0.013	0.0000	0.0000, 0.0023	0.000
2-year old	0.161	0.034	0.0111	0.0034, 0.0380	0.654
Adult	0.321	0.030	0.0115	0.0053, 0.0317	0.334

^aCoefficient of process variation computed as $\hat{\sigma}_{spatial}/\bar{b}$

provinces (Table 17). Even years had almost twice the fecundity of odd years (Table 17). However, models $\{b_{prov+eo}\}$, $\{b_{prov*eo}\}$ and $\{b_{prov+t}\}$ were weighted almost equally, based on Akaike weights (Table 16). The remaining models had Akaike weights of zero indicating they poorly explained the fecundity data. Thus, there appeared to be a province effect and a time effect. However, there was some uncertainty whether the time effects were an even-odd year effect or just a variable time effect (t). There was no evidence of a linear trend in fecundity, and ownership did not appear to influence fecundity. Additional tests of effects corroborated these results based on model selection. A test for no interaction among provinces and years was significant ($P = 0.001$) indicating differences among provinces were not consistent among year and there was no evidence of interaction between ownership class and year ($P = 0.994$). There was evidence of differences among years ($P = 0.0001$), and among even-odd years ($P = 0.0001$), but no evidence of differences among ownership classes ($P = 0.342$).

The meta-analysis of the 8 monitoring areas produced results similar to those of the 15 study areas (Table 16). Again, model $\{b_{prov+eo}\}$ was selected as the best model with models $\{b_{prov*eo}\}$ and $\{b_{prov+t}\}$ having somewhat lower but similar weights. The remaining models had Akaike weights of zero and were not considered as meaningful alternatives. Model $\{b_{prov+eo}\}$ yielded similar estimates for provinces and even and odd years as the model $\{b_{prov+eo}\}$ from the meta-analysis of the 15 study areas. Again, there was no evidence to support any linear trends in fecundity over time (Table 16). The test for no interaction among provinces and years was significant ($P = 0.009$) indicating that differences among the provinces were not consistent among years. There was no evidence of interaction between ownership class and year ($P = 0.960$), but there was evidence of differences among years ($P = 0.0001$), among even and odd

years ($P = 0.0001$), and weak evidence of differences in the mean among ownership classes ($P = 0.067$) with "mixed ownership" having a slightly higher estimated mean number fledged than the U. S. Forest Service/National Park ownership. However, based on the model selection results (Table 16), there was little evidence that ownership contributed much to the variation in the data.

There was no evidence that differences in field protocols affected estimates of fecundity (Table 16). The best model $\{b_{eo}\}$ indicated an even-odd year effect and was 10.5 times as likely as the second-ranked model $\{b_{proto+eo}\}$, which included the protocol effect (Table 16). Estimates from model $\{b_{eo}\}$ were similar to the best models from the 15 study area and 8 monitoring area meta-analyses (Table 17). A test for no interaction between protocols and years was not significant ($P = 0.811$) indicating that differences among protocols may be consistent among years. There was strong evidence for differences among years ($P = 0.0001$), and between even/odd years ($P = 0.0001$), but not among protocols ($P = 0.146$).

TABLE 16. Model selection criteria for meta-analysis of fecundity (b) for adult female Northern Spotted Owls on 15 study areas, eight monitoring areas and for protocols to determine reproduction on 13 study areas.

Model	K^a	AIC)	w_i^b
<i>Meta-analysis of Study Areas (15 areas)</i>				
$b_{\text{prov+eo}}$	7	16420.50	0.00	0.362
$b_{\text{prov*eo}}$	10	16420.70	0.20	0.327
$b_{\text{prov+t}}$	19	16420.80	0.30	0.311
b_{eo}	4	16437.58	17.08	0.000
$b_{\text{prov*t}}$	49	16452.90	32.40	0.000
$b_{\text{owner+eo}}$	6	16454.30	33.80	0.000
b_t	16	16459.20	38.70	0.000
$b_{\text{owner*eo}}$	8	16461.90	41.40	0.000
$b_{\text{owner+t}}$	18	16468.30	47.80	0.000
$b_{\text{prov+T}}$	7	16480.50	60.00	0.000
b_T	4	16497.20	76.70	0.000
$b_{\text{prov*T}}$	10	16498.50	78.00	0.000
$b_{\text{owner*t}}$	39	16518.20	97.70	0.000
$b_{\text{owner*T}}$	8	16519.50	99.00	0.000
<i>Meta-analysis of Monitoring Areas (8 areas)</i>				
$b_{\text{prov+eo}}$	6	11410.90	0.00	0.461
$b_{\text{prov+t}}$	18	11411.70	0.80	0.309
$b_{\text{prov*eo}}$	8	11412.30	1.40	0.229
b_{eo}	4	11427.60	16.70	0.000
$b_{\text{owner+eo}}$	5	11430.30	19.40	0.000
$b_{\text{owner*eo}}$	6	11434.10	23.20	0.000
$b_{\text{prov*t}}$	40	11436.50	25.60	0.000
b_t	16	11439.00	28.10	0.000
$b_{\text{owner+t}}$	17	11441.40	30.50	0.000
$b_{\text{prov+T}}$	6	11455.40	44.50	0.000
b_T	4	11464.50	53.60	0.000
$b_{\text{prov*T}}$	8	11467.20	56.30	0.000
$b_{\text{owner*t}}$	30	11472.50	61.60	0.000
$b_{\text{owner*T}}$	6	11474.70	63.80	0.000
<i>Meta-analysis of Protocol (13 areas)</i>				
b_{eo}	4	15769.00	0.00	0.900
$b_{\text{proto+eo}}$	5	15773.70	4.70	0.086
$b_{\text{proto*eo}}$	6	15777.40	8.40	0.013
b_t	16	15782.60	13.60	0.001
$b_{\text{proto+t}}$	17	15786.00	17.00	0.000
$b_{\text{proto*t}}$	25	15805.10	36.10	0.000
b_T	4	15814.40	45.40	0.000
$b_{\text{proto+T}}$	5	15818.20	49.20	0.000
$b_{\text{proto*T}}$	6	15824.00	55.00	0.000

^aNumber of parameters

^bAkaike weights

TABLE 17. Estimates of fecundity (b) for adult female Northern Spotted Owls from minimum AIC models selected in meta-analyses of 15 study areas, 8 monitoring areas, and 13 study areas examined for differences in field protocols used to determine reproduction.

Effect	$\{b_{\text{prov+eo}}\}$ from 15 study areas		$\{b_{\text{prov+eo}}\}$ from monitoring areas		$\{b_{\text{eo}}\}$ from protocol analysis	
	\hat{b}	$\text{se}(\hat{b})$	\hat{b}	$\text{se}(\hat{b})$	\hat{b}	$\text{se}(\hat{b})$
Douglas-fir province	0.2757	0.0186	0.3026	0.0206	— ^a	—
East Slope province	0.5159	0.0301	0.5847	0.0472	—	—
Mixed Conifer province	0.3361	0.0234	0.3610	0.0240	—	—
Redwood province	0.3435	0.0481	— ^b	—	—	—
Even year	0.4819	0.0199	0.5289	0.0238	0.4504	0.0206
Odd year	0.2536	0.0210	0.3033	0.0244	0.2293	0.0217

^aNo province effect in this model.

^bNo study areas from the redwood province were included in this analysis.

RATES OF POPULATION CHANGE

Estimates of \mathcal{S}_{PM}

Estimates of \mathcal{S}_{PM} for the 15 study areas ranged from 0.828 to 0.984 (Table 18). These estimates of \mathcal{S}_{PM} may be biased low because they were based on estimates of juvenile survival that were uncorrected for emigration. With the exception of the AST study area, estimates of \mathcal{S}_{PM} were precise (Table 18). Ninety-five percent confidence intervals overlapped 1 for four of the study areas (AST, KLA, RAI, TYE) providing some evidence that the average survival and fecundity rates for those areas produced a stationary population during the periods of study. However, the low precision in $\hat{\lambda}_{\text{PM}}$ for AST makes this conclusion questionable for this study area. The remaining 12 study areas had upper 95% confidence intervals for $\hat{\lambda}_{\text{PM}}$ that were less than one. Overall, an estimate of \mathcal{S}_{PM} averaged across 15 of the study areas (excluding COA) suggested a significant annual population decline of 8.3% (Table 18). Spatial variation in the estimates of \mathcal{S}_{PM} was low with a coefficient of process variation of 0.049 ($\hat{\sigma}_{\text{spatial}}^2 = 0.00203$, 95% CI = 0.00091, 0.00563).

TABLE 18. Estimates of the annual rate of population change, λ_{PM} , for female Northern Spotted Owls on 16 independent study areas throughout their range.

Study area	$\hat{\lambda}_{PM}$	$\hat{se}(\hat{\lambda}_{PM})$	CV_{sampling}	95% Confidence intervals	
				Lower	Upper
AST	0.9195	0.0773 ^a	0.084	0.7680	1.0710
CAS ^b	0.8464	0.0206	0.024	0.8060	0.8868
CLE	0.9406	0.0226	0.024	0.8963	0.9848
COA	0.9702	0.0144	0.015	0.9420	0.9984
EEU ¹	0.8279	0.0205	0.025	0.7877	0.8681
ELC	0.9724	0.0137	0.014	0.9455	0.9992
HJA ^b	0.9254	0.0142	0.015	0.8976	0.9532
HUP	0.8793	0.0337	0.038	0.8132	0.9454
KLA	0.9588	0.0211	0.022	0.9174	1.0002
NWC	0.9511	0.0145	0.015	0.9228	0.9795
OLY ^b	0.8763	0.0160	0.018	0.8449	0.9077
RAI ^c	0.9395	0.0313	0.033	0.8781	1.0008
SIM	0.9686	0.0150	0.015	0.9393	0.9979
TYE	0.9835	0.0199	0.020	0.9444	1.0226
WEN ^b	0.8796	0.0145	0.016	0.8512	0.9080
WSR	0.8685	0.0246	0.028	0.8203	0.9168
Mean	0.9167 ^d	0.0131 ^d	--	0.8886 ^e	0.9448 ^e

^a \hat{b}_1 and $\hat{se}(\hat{b}_1)$ set to 0 because estimates were lacking.

^b $\hat{\lambda}_{pm}$ calculated based on 4-age class survival model.

^c Juvenile survival used to estimate λ was average of WEN and CLE study areas.

^d Weighted mean and standard error from 15 study areas (COA not included because this area was part of ELC)

^e Confidence intervals calculated with empirical standard deviation and t -distribution with 14 df .

TABLE 19. Estimates of \mathcal{S}_{PM} based on juvenile survival adjusted for emigration ($\hat{\lambda}_{PM}|\hat{\mathcal{S}}_0$) for CLE, OLY, and TYE study areas.

Study area	$\hat{\lambda}_{PM}^a$	$\hat{\lambda}_{PM} \hat{\mathcal{S}}_0$	$se(\hat{\lambda}_{PM} \hat{\mathcal{S}}_0)$	95% confidence intervals
CLE	0.9406	1.0190	0.0406	0.9394, 1.0986
OLY	0.8763	0.9407	0.0196	0.9023, 0.9790
TYE	0.9835	1.0241	0.0254	0.9742, 1.0739

^aFrom Table 18.

Estimates of \mathcal{S}_{PM} increased 4.1 to 8.3% when we used radio-telemetry data to adjust for juvenile emigration on the three areas (TYE, CLE, OLY) where we had data from radio-marked juveniles (Table 19). In two of the three study areas (CLE and TYE), $\hat{\lambda}_{PM}$ was greater than one although 95% confidence intervals still overlapped $\mathcal{S} = 1$ indicating these populations were probably stationary and not increasing. However, the OLY study area still yielded a $\hat{\lambda}_{PM}$ that indicated a declining population (Table 19).

We used two other approaches to examine the effect of biased estimates of juvenile survival on $\hat{\lambda}_{PM}$. First, we examined the effect of estimated average emigration rates on the average estimate of juvenile survival combined with the averages of fecundity and non-juvenile survival to compute an average estimate of \mathcal{S}_{PM} . Second, we estimated the juvenile emigration rates required to achieve a stationary population and compared them with rates estimated from the three study areas where radio-telemetry data were available. In the first approach, we used the average estimates of age-specific survival for non-juveniles from Table 9 and the age-specific fecundity estimates from Table 15. We also used the estimate of mean juvenile apparent survival from Table 9 and adjusted it by the mean emigration rate from Table 10 to obtain an estimate of juvenile survival ($\bar{\mathcal{S}}_0 = 0.442 [0.057]$). We used these estimates to estimate the mean \mathcal{S}_{PM} with a four-age class Leslie matrix, and we used the sampling variances of the survival and fecundity estimates with the average of the sampling correlations and covariances across the study areas to estimate a standard error for the mean \mathcal{S}_{PM} using the delta method. Based on this approach, we obtained $\bar{\lambda}_{PM} = 0.961$, $se(\bar{\lambda}_{PM}) = 0.017$, and 95% confidence intervals of 0.925, 0.997 (using t -statistic based on 14 df). This estimate indicated an overall decline in territorial females of 3.9% per year that was different from a stationary population based on the 95% confidence interval.

In the second approach, we estimated the juvenile emigration rate necessary to achieve a stationary population (i.e., $\mathcal{S} = 1$) as:

$$\hat{E}_{0|\lambda=1} = 1 - \frac{\hat{\phi}_0}{\hat{S}_{0|\lambda=1}},$$

where $\hat{S}_{0|\lambda=1}$ is the estimate of juvenile survival necessary to achieve a stationary population (based on setting $\mathcal{S} = 1$ in the characteristic equation, leaving all parameter estimates other than mean juvenile survival the same, and solving for $\hat{S}_{0|\lambda=1}$). We did not compute standard errors for these estimates but merely viewed them as bench-marks against which to examine how much undetected juvenile emigration would have to occur to produce an estimate of $\mathcal{S} = 1$. The estimates of $\hat{E}_{0|\lambda=1}$ for 11 of the study areas ranged from 0.141 to 0.855 (Table 20). For three of

TABLE 20. Estimates of juvenile survival ($\hat{S}_{0|\lambda=1}$) and emigration rates ($\hat{E}_{0|\lambda=1}$) needed to achieve stationary populations ($\mathcal{S} = 1$) of female Northern Spotted Owls on 14 study areas throughout their range. RAI not included because juvenile survival was not estimated for this study area.

Study area	$\hat{\lambda}_{PM}^a$	$\hat{S}_{0 \lambda=1}$	$\hat{E}_{0 \lambda=1}$
AST	0.9195	0.8371	0.5485
CAS	0.8464	1.6453	— ^b
CLE	0.9406	0.3232	0.3966
EEU	0.8279	8.0329	— ^b
ELC	0.9724	0.5358	0.2646
HJA	0.9254	0.8151	0.6258
HUP	0.8793	1.2440	— ^b
KLA	0.9588	0.5014	0.2740
NWC	0.9511	0.4787	0.3837
OLY	0.8763	0.9357	0.7307
SIM	0.9686	0.4907	0.2562
TYE	0.9835	0.5191	0.1408
WEN	0.8796	0.6008	0.7620
WSR	0.8685	0.4409	0.8548

^aFrom Table 18.

^bEstimates unrealistic because $\hat{S}_{0|\lambda=1} > 1$.

the study areas (CAS, EEU, and HUP), $\hat{S}_{0|\lambda=1}$ was >1 indicating that these populations would never achieve $\mathcal{S} = 1$ during their period of study even with $S_0 = 1$ (given all other parameters are well estimated). Therefore, we did not estimate emigration rates for these study areas. For the 12 study areas where we did obtain estimates of $E_{0|\mathcal{S}=1}$, we estimated a mean of 0.476, which was higher than the mean \hat{E} estimated from radio-telemetry data (Table 10). This suggested that, on average, current estimates of juvenile emigration rates based on radio-telemetry would not be sufficient to achieve a stationary population. However, there was considerable variation in study areas in both estimated emigration rates and $E_{0|\mathcal{S}=1}$. Thus, \mathcal{S}_{PM} for some study areas may be underestimated when in fact they

TABLE 21. Estimates of average \mathcal{S}_{RJS} ($\bar{\lambda}_{\text{RJS}}$) for female Northern Spotted Owls on 12 study areas in Washington, Oregon, and California. Starred study areas are those based on density study areas; unstarred study areas are based on individual owl territories. For time-specific models, estimates of $\bar{\lambda}_{\text{RJS}}$ are averages across years (see text for explanation).

Study area	\hat{c}	Model ^a	$\bar{\lambda}_{\text{RJS}}$	$\text{se}(\bar{\lambda}_{\text{RJS}})$	CV ^b	95% Confidence intervals	
						Lower	Upper
CAS	1.864	$\{\mathcal{N}_t, p_., \mathcal{S}_t\}$	1.0041	0.0934	0.093	0.8210	1.1872
COA	1.679	$\{\mathcal{N}_t, p_T, \mathcal{S}_t\}$	1.0012	0.0455	0.045	0.9121	1.0903
*ELL	1.547	$\{\mathcal{N}_t, p_{s+t}, \mathcal{S}_t\}$	1.0151	0.0239	0.024	0.9683	1.0619
*HJA	1.170	$\{\mathcal{N}_t, p_t, \mathcal{S}_{\text{INT}}\}$	1.0073	0.0220	0.022	0.9641	1.0505
*HUP	1.384	$\{\mathcal{N}_t, p_{s+E}, \mathcal{S}_t\}$	0.9774	0.0315	0.032	0.9156	1.0391
KLA	1.135	$\{\mathcal{N}_t, p_., \mathcal{S}_t\}$	1.0086	0.0405	0.040	0.9293	1.0879
*NWC	1.094	$\{\mathcal{N}_t, p_{c+w}, \mathcal{S}_t\}$	0.9979	0.0133	0.013	0.9718	1.0240
*OLY	1.142	$\{\mathcal{N}_t, p_., \mathcal{S}_t\}$	1.0019	0.0392	0.039	0.9252	1.0786
RAI	1.446	$\{\mathcal{N}_t, p_t, \mathcal{S}_T\}$	0.9686	0.0854	0.088	0.8013	1.1360
*SIM	1.255	$\{\mathcal{N}_t, p_s, \mathcal{S}_t\}$	1.0271	0.0771	0.075	0.8759	1.1782
*TYE	1.122	$\{\mathcal{N}_t, p_{s+T}, \mathcal{S}_t\}$	0.9860	0.0151	0.015	0.9564	1.0156
WSR	1.501	$\{\mathcal{N}_t, p_., \mathcal{S}_{\text{INT}}\}$	0.9990	0.0268	0.027	0.9465	1.0520

^aBest capture-recapture model structure from program MARK; overall model is best selected model.

^bCoefficient of sampling variation.

are stationary whereas others may never achieve a stationary population even when juvenile emigration rates are included.

Estimates of \mathcal{S}_{RJS}

Estimates of \mathcal{S}_{RJS} for the 12 study areas ranged from 0.969 (RAI) to 1.027 (SIM) with a weighted mean of 0.997 ($\text{se}(\bar{\lambda}) = 0.003$; 95% confidence intervals = 0.991, 1.004) (Table 21). Three study areas (CAS, RAI, and SIM) yielded $\hat{\lambda}_{\text{RJS}}$ that were much less precise than the other

areas, suggesting that point estimates from these areas should be viewed with some skepticism. For example, $\hat{\lambda}_{\text{RJS}}$ for SIM was 1.027 indicating a population growing by 2.7% a year. However, the 95% confidence intervals were between 0.876 and 1.178 indicating considerable uncertainty in this estimate (Table 21). The lack of precision in some estimates was accounted for in calculating the weighted mean. None of the estimates of λ_{RJS} was different from $\lambda = 1$, based on their 95% confidence intervals. Differences between $\hat{\lambda}_{\text{RJS}}$ and $\hat{\lambda}_{\text{PM}}$ ranged from 0.003 (TYE) to 0.126 (OLY). Point estimates of λ_{RJS} and λ_{PM} agreed most closely for the TYE ($\hat{\lambda}_{\text{PM}} = 0.984$ from Table 18; $\hat{\lambda}_{\text{RJS}} = 0.986$ from Table 21). The data from five of the study areas were best described by a variable time structure on λ (i.e., λ_t) whereas data from four of the study areas was best described by a model with no time structure (i.e., λ) (Table 21). Three of the study areas had linear (λ_t) or pseudo-threshold (λ_{INT}) trends in λ_{RJS} over time. In all three cases, trends in λ_{RJS} were negative, substantial and different from zero; $\hat{\beta} = -0.111$ for the HJA (95% CI = -0.194, -0.027), $\hat{\beta} = -0.282$ for the RAI (95% CI = -0.496, -0.069), and $\hat{\beta} = -0.162$ for the WSR (95% CI = -0.319, -0.005). These negative trends indicated that annual rates of population change were declining on the three areas.

DISCUSSION

We found several important results in the process of analyzing the demographic data for Northern Spotted Owls. First, the negative trend in survival of adult females reported by Burnham et al. (1994) was no longer apparent with the addition of five more years of data. This change coincided with substantial changes in forest management (e.g., implementation of the Northwest Forest Plan), but could not be explicitly attributed to those changes. Second, the range-wide estimate for the rate of population change using the Leslie projection matrix (λ_{PM}) indicated that Northern Spotted Owl populations were, on average, still declining by 3.9% per year. This estimate included juvenile survival estimates adjusted for emigration. However, this average estimate of decline should be viewed in the context of the variation in estimates of λ_{PM} across studies. Some areas approached a stationary population given appropriate estimates of juvenile emigration, whereas other areas were not likely to attain a stationary population. The latter conclusion resulted from high estimates of juvenile survival or emigration required to achieve estimates of λ close to a stationary population (i.e., $\lambda = 1$).

TRENDS IN DEMOGRAPHIC PARAMETERS

We found no consistent annual trends in fecundity or apparent survival of adult females, based on the meta-analyses of these two parameters. The meta-analyses had considerably more statistical precision for detecting region-wide trends than did the individual study area analyses. However, small scale differences among study areas tended to be eliminated because of the large number of study areas involved. This partially explains the disparity between the 15-area and 8-area meta-analyses of adult female survival in terms of study area effects. The 15-area meta-analysis found no study area effects whereas the 8-area meta-analysis did (Tables 11 and 12; Fig. 5). With the large number of areas in the 15-area analysis, it was unlikely that a group effect would become evident because more groups were probably similar in their effect than dissimilar. For the 15-area analysis, a model with a study areas effect would require 14 additional parameters whereas only seven additional parameters were required for the 8-area analysis. Regardless, both analyses exhibited the same time-dependent variation in apparent survival with no evidence of a linear, pseudo-threshold or quadratic time trend. The pattern of annual survival estimates from 1985 through 1992 (Fig. 5) was similar to the pattern that yielded the significant, negative time trend in adult female survival reported by Burnham et al. (1994; see their Fig. 2). However, since that reported decline, estimates of apparent survival for adult females increased, at least from the larger range-wide perspective. This is an important result because estimates of δ_{PM} are most sensitive to survival of adults (Noon and Biles 1990). Whether the changing trend in adult female apparent survival is directly related to changes in forest management is unknown. The change coincides with the listing of the owl and subsequent adoption of the Northwest Forest Plan that curtailed harvesting of late-successional forests on public lands. However, we cannot ascribe cause and effect based on this association.

Results from some of the study area analyses partially support the results of the meta-analysis of adult female survival. Most (11 of 15) study areas supported a model structure where apparent survival for adult females or non-juveniles either varied over time, had positive linear trends over time, or, in one case (TYE), had a quadratic trend where survival decreased in early years and then increased in later years (Tables 7 and 8). With the exception of the KLA study area, studies exhibiting a positive linear trend in annual survival were short-term (since 1990) with respect to the patterns observed in the meta-analysis. That is, these studies were conducted during the period that captured the increase in survival following the decline observed by Burnham et al. (1994). Overall, apparent survival probabilities for adult females were high (>0.80) and exhibited little variation across study areas (Table 9). The one contrary trend was with the studies in California. The best model for all three studies in California supported a

negative trend in non-juvenile survival; on one study (HUP) this estimated decline was dramatic (Table 8; Fig. 4). The data from the individual study areas did not support much variation in juvenile survival over time, even though such variation undoubtedly exists. Only three studies supported a negative trend in juvenile survival. Again, two of these studies were in California. Overall, estimates of juvenile apparent survival, unadjusted for emigration, were low but exhibited considerably more variation across study areas than did non-juvenile survival (Table 9).

Fecundity appeared to vary over time with evidence for a bi-annual cycle (the even/odd year effect; Table 16). Unlike the meta-analyses for apparent survival, there appeared to be differences between provinces, with the East Slope province having higher fecundity than the other provinces (Table 7). The lack of a consistent time trend across the range of the owl was similar to the results of the 1993 analysis (Burnham et al. 1994). The cyclic pattern in fecundity appeared to be much more pronounced starting in 1990 (Fig. 2) and may be weather or prey related, which is a topic for further analysis and research.

TRENDS IN RATES OF POPULATION CHANGE

Based on Projection Matrices

There were several important considerations in assessing the results of rates of population change based on projection matrices (λ_{PM}). First, λ_{PM} was an average annual rate of change for territorial, female Northern Spotted Owls if the conditions during the time period of investigation were maintained indefinitely (Franklin et al. 1996). In other words, λ_{PM} represented an average over a specific time period and place and did not predict rates of population change beyond the time period during which it was measured. Second, λ_{PM} refers to the resident, territorial population and addresses the question: *have the resident territorial females replaced themselves?* (Burnham et al. 1994).

The mean estimate of λ_{PM} from the combined study areas indicated that Northern Spotted Owl populations were declining by 8.3% a year (Table 18). When adjusted for juvenile emigration, λ_{PM} estimated from average parameters across studies still indicated a population declining by 3.9% a year. However, these averages did not reflect the variation in λ_{PM} estimated for the individual areas. Based on the projection matrix estimates without adjustment for juvenile emigration, only one study area (TYE) yielded an estimate of λ_{PM} suggested a stationary population (Table 18). The point estimate for this study area was precise, close to $\lambda = 1$ and had 95% confidence intervals that substantially overlapped $\lambda = 1$. While the 95% confidence intervals for $\hat{\lambda}_{PM}$ included $\lambda = 1$ for three other study areas, two of the areas (KLA and RAI) had

confidence intervals barely including $\mathcal{S} = 1$ and one area (AST) yielded $\hat{\lambda}_{\text{PM}}$ that was imprecise relative to the other areas (Table 18). For the three areas where we were able to adjust estimates of \mathcal{S}_{PM} , two areas (CLE and TYE) indicated a stationary population while the third area (OLY) did not (Table 19).

Concerning the remaining study areas, certain conclusions can be tentatively suggested based on estimates of $\mathcal{S}_{0|\lambda=1}$ and $E_{0|\lambda=1}$ (Table 20). First, at least six areas (AST, CAS, EEU, HJA, HUP, OLY) were not stationary during the period we measured \mathcal{S}_{PM} because $\mathcal{S}_{0|\lambda=1}$ would need to be greater than 0.80, given all other parameter estimates are unbiased. Although such levels of juvenile survival may be achieved in a single year, average estimates of that magnitude have never been observed in Northern Spotted Owls. Second, 6 additional areas (CLE, ELC, KLA, NWC, SIM, TYE) had estimates of $E_{0|\lambda=1}$ that were within the range of juvenile \hat{E} estimated through radio-telemetry (Tables 10 and 20). In these cases, it is conceivable that populations on these areas could approach a stationary population. However, the estimated declines in juvenile and non-juvenile survival in the California studies suggested that these areas were experiencing accelerated population declines (see Burnham et al. 1994). Changing weather conditions was one potential factor for these declines in survival because Franklin (1997) found that weather conditions strongly influenced variation in non-juvenile survival and recruitment rates in Northern Spotted Owls in California.

A further complication was that adjustments for juvenile apparent survival based on \hat{E} could be positively biased because capture-recapture estimates for most studies already incorporate some emigration. Juvenile capture histories for most areas included juveniles that were recaptured off the study area. In these cases, $\hat{E}_{0|\lambda=1}$ (Table 20) represented *additional* juvenile emigration (above that already included in juvenile apparent survival) required to achieve a stationary population for a given area. Thus, $\hat{\lambda}_{\text{PM}}$ would be less biased by juvenile emigration and fewer of the seven studies we suggested could be stationary would, in fact, be stationary. The separation of juvenile emigration already accounted for in estimates of juvenile survival and that estimated by radio-telemetry were beyond the scope of this workshop but needs to be examined in more detail (see Further Considerations).

Thus, the results concerning rates of population change based on \mathcal{S}_{PM} on individual study areas are a mixture of declining populations, potentially stationary populations and, at least one population that appeared to be stationary. Overall, the estimate of \mathcal{S}_{PM} computed from average parameters and adjusted for emigration is the best approximation we had for a range-wide estimate of rate of population change for Northern Spotted Owls. That is, we think our best estimate of apparent range-wide population decline was 3.9% per year. This rate was lower than the rate (4.5%) estimated in the previous analysis (Burnham et al. 1994).

Based on the Reparameterized Jolly-Seber Estimator

The mean estimate of \mathcal{G}_{RJS} indicated that Northern Spotted Owl populations were essentially stationary during the period studied. This suggests that either 1) there were sufficient juveniles produced and recruited into the territorial population on these areas to achieve a stationary population or 2) there was sufficient immigration from either outside the areas or from floaters within the area (or both) to replace losses due to death and emigration. Thus, study areas with an estimate of $\mathcal{G}_{\text{RJS}} \approx 1$ could reflect self-sustaining stationary populations, populations requiring substantial immigration to maintain stability (the “rescue” effect; Gotelli 1991), or a combination of both. A problem with estimation of recruitment using current models for \mathcal{G}_{RJS} is that local recruitment (recruitment into an area of new, territorial individuals born on the area) cannot be separated from recruitment due to immigration from outside of the study area.

There were two problems in comparing the estimates of \mathcal{G}_{RJS} and \mathcal{G}_{PM} . First, there were differences in the definitions of the two parameters: \mathcal{G}_{RJS} was defined as the rate of change in abundance of territorial females exposed to sampling efforts, whereas \mathcal{G}_{PM} was the rate of change of territorial females based on estimated survival probabilities and fecundity. The key difference was that \mathcal{G}_{RJS} included immigration from outside study areas, whereas \mathcal{G}_{PM} did not. While \mathcal{G}_{PM} addressed the question “*were the resident, territorial females replacing themselves?*”, \mathcal{G}_{RJS} addressed the question “*had the resident, territorial females been replaced?*”. Second, the study areas used to estimate \mathcal{G}_{RJS} were a subset of the areas used to estimate \mathcal{G}_{PM} . This made comparability between the two types of estimates difficult.

There were a number of potential biases with \mathcal{G}_{RJS} due to sampling Northern Spotted Owls (Appendix D). One such bias, expansion of study areas over time, related to initial years of surveys on the study areas. If owls were missed in the first years of the study, when observers were first learning their respective study areas, then \mathcal{G}_{RJS} estimates for those initial years will be biased high. We did not account for this “learning curve” when estimating \mathcal{G}_{RJS} but could have by eliminating the first two years in some data sets. In addition, the constraints on p could cause additional process variance on \mathcal{G}_{RJS} to be larger. In hindsight, we should have used a time-varying (t) structure on p for all study areas. We chose not to correct these problems in estimating \mathcal{G}_{RJS} after the workshop so as not to violate the intent of the protocol established during the workshop. We believe that the approach for estimating \mathcal{G}_{RJS} has considerable utility for use with capture-recapture data from Northern Spotted Owls. However, additional work needs to be done in understanding how sampling Northern Spotted Owl populations affects the estimates of \mathcal{G}_{RJS} obtained from such analyses.

FURTHER CONSIDERATIONS

As with any extensive scientific endeavor, a number of issues remain that need to be dealt with either in further analyses of the data sets used here or in future workshops. We feel that the following issues need attention:

- 1) Relationships between demographic parameters and management strategies for Northern Spotted need further examination. Such analyses should include examination of landscape-scale vegetation features of study areas in relation to rates of population change and inclusion of covariates, such as habitat loss rates, in meta-analyses of adult female survival.
- 2) Relationships between demographic parameters and external covariates, such as weather and habitat, should be investigated at a larger scale to gain further insights into ecological mechanisms affecting Northern Spotted Owl populations. This would require considerable thought about appropriate choice of covariates and model structures.
- 3) Better estimators of juvenile emigration rates are needed. Multi-strata capture-recapture models (Hestbeck et al. 1991) provide potential capture-recapture estimators, possibly in combination with radio-telemetry data. An emphasis should also be made to estimate annual juvenile survival using radio-telemetry data on all study areas.
- 4) Better estimators of \mathcal{S}_{RJS} that allow separation of local recruitment from immigration are needed. This may entail further theoretical development of these, and related, estimators.

ACKNOWLEDGMENTS

David Anderson provided considerable input and effort into the development and organization of this workshop. We are particularly indebted to Jennifer Blakesley, Mary Connor, Stephen J. Dinsmore, Greg Phillips, Eric Rexstad, Daniel Rosenberg and Tanya Shenk for their assistance during and after the workshop. They worked hard and made it fun. Pete Loschl, Janice Reid, and Stan Sovern did an excellent job in checking all the data used in the workshop. Jennifer Blakesley, Mary Connor, Pete Loschl, Janice Reid, and Stan Sovern assisted with manuscript preparation. Janice Reid prepared the study area maps. Melani Bonnichsen (Oregon Cooperative Research Unit), and Beverly Klein and Karen Adleman (Colorado Cooperative Research Unit) provided excellent administrative support. In particular, we thank

all the biologists (see Appendix A) that brought their data for analysis and weathered the entire workshop session with good humor. We are also indebted to the many dedicated field workers who collected so much data on Northern Spotted Owls. Although we cannot name them all, they should be proud of their contributions to this effort. Funding for demographic studies of Northern Spotted Owls on federal lands was provided primarily by the U. S. Forest Service, U. S. Bureau of Land Management, and National Park Service. Funding for the workshop was provided by the U. S. Fish and Wildlife Service, U. S. Bureau of Land Management, U. S. Forest Service, and U. S. Geological Survey Forest and Rangeland Ecosystem Sciences Center.

LITERATURE CITED

- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267-281 in B. N. Petrov and F. Csaki, editors. Second International Symposium on Information Theory. Akademiai Kiado, Budapest, Hungary.
- Akaike, H. 1985. Prediction and entropy. Pages 1-24 in A. C. Atkinson and S. E. Fienberg, editors. A celebration of statistics. Springer, New York, New York, USA.
- Alvarez-Buylla, E. R., and M. Slatkin. 1994. Finding confidence limits on population growth rates: three real examples revised. *Ecology* 75:255-260.
- Anderson, D. R., and K. P. Burnham. 1992. Demographic analysis of Northern Spotted Owl populations. Recovery Plan for the Northern Spotted Owl, Appendix C. U. S. Fish and Wildlife Service, Portland, Oregon, USA.
- Anderson, D. R., and K. P. Burnham. 1994. AIC model selection in overdispersed capture-recapture data. *Ecology* 75: 1780-1793.
- Buckland, S. T., K. P. Burnham, and N. H. Augustin. 1997. Model selection: an integral part of inference. *Biometrics* 53:603-618.
- Burnham, K. P. In preparation. Random effects models in ringing and capture-recapture studies.
- Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.
- Burnham, K. P., D. R. Anderson, and G. C. White. 1994. Estimation of vital rates of the Northern Spotted Owl. Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, Colorado, USA.
- Burnham, K. P., D. R. Anderson, and G. C. White. 1996. Meta-analysis of vital rates of the Northern Spotted Owl. *Studies in Avian Biology* 17:92-101.

- Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society, Monograph 5. 437pp.
- Carothers, A.D. 1973. The effects of unequal catchability on Jolly-Seber estimates. *Biometrics* 29:79-100.
- Caswell, H. 1989. Matrix population models. Sinauer Associates, Inc. Sunderland, Massachusetts, USA.
- Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. *Biometrika* 51:429-438.
- Evans, M., N. Hastings, and B. Peacock. 1993. Statistical distributions, second edition. John Wiley and Sons, New York, New York, USA.
- FEMAT (Forest Ecosystem Management Assessment Team). 1993. Forest ecosystem management: an ecological, economic, and social assessment. U.S. Department of Agriculture and U.S. Department of Interior, Portland, Oregon, USA.
- Forsman, E. D. 1983. Methods and materials for locating and studying spotted owls. United States Forest Service Technical Report PNW-162, Portland, Oregon, USA.
- Forsman, E. D., A. B. Franklin, F. M. Oliver, and J. P. Ward. 1996. A color band for spotted owls. *Journal of Field Ornithology* 67:507-510.
- Forsman, E. D., E. C. Meslow, and H. M. Wight. 1984. Distribution and biology of the Spotted Owl in Oregon. *Wildlife Monographs* 87:1-64.
- Forsman, E.D. and E.C. Meslow. 1986. The spotted owl. Pages 742-761 in Audubon Wildlife Report: 1986. National Audubon Society, New York, New York, USA.
- Franklin, A. B. 1997. Factors affecting temporal and spatial variation in northern spotted owl populations in northwest California. Dissertation. Colorado State University, Fort Collins, Colorado, USA.
- Franklin, A. B., D. R. Anderson, E. D. Forsman, K. P. Burnham, and F. F. Wagner. 1996. Methods for collecting and analyzing demographic data on the Northern Spotted Owl. *Studies in Avian Biology* 17:12-20
- Gotelli, N. J. 1991. Metapopulation models: the rescue effect, the propagule rain, and the core-satellite hypothesis. *American Naturalist* 138: 768-776.

- Gutiérrez, R. J., A. B. Franklin, and W. S. Lahaye. 1995. Spotted Owl. A. Poole and F. Gill, editors. The birds of north America 179. The Academy of Natural Sciences, Philadelphia, PA and The American Ornithologists' Union, Washington, DC, USA.
- Gutiérrez, R. J., E. D. Forsman, A. B. Franklin, and E. C. Meslow. 1996. History of demographic studies in the management of the Northern Spotted Owl. *Studies in Avian Biology* 17:6-11.
- Hetsbeck, J. B., J. D. Nichols, and R. A. Malecki. 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. *Ecology* 72: 523-533.
- Hurvich, C. M., and C.-L. Tsai. 1989. Regression and time series model selection in small samples. *Biometrika* 76: 297-307.
- Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration--stochastic model. *Biometrika* 52:225-247.
- Lande, R. 1988. Demographic models of the Northern Spotted Owl. *Oecologia* 75: 601-607.
- Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67-118.
- Leslie, P. H. 1945. On the use of matrices in certain population mathematics. *Biometrics* 21:1-18.
- Leslie, P. H. 1948. Some further notes on the use of matrices in population mathematics. *Biometrika* 33:183-212.
- Lint, J., B. Noon, R. Anthony, E. Forsman, M. Raphael, M. Collopy, and E. Starkey. 1999. Northern spotted owl effectiveness monitoring plan for the Northwest forest plan. U. S. Forest Service General Technical Report PNW-GTR-440. 43pp.
- Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS® system for mixed models. SAS Institute, Inc., Cary, North Carolina, USA.
- McDonald, D. B., and H. Caswell. 1993. Matrix methods for avian demography. Pages 139-185 In D. M. Power, editor. Current ornithology, volume 10. Plenum Press, New York, New York, USA.
- Meslow, E. C. 1993. Spotted owl protection: unintentional evolution toward ecosystem management. *Endangered Species Update* 3/4:34-38.

- Moen, C. A., A. B. Franklin, and R. J. Gutiérrez. 1991. Age determination of subadult Northern Spotted Owls in northwest California. *Wildlife Society Bulletin* 19:489-493.
- Nichols, J.D., J.E. Hines, and K.H. Pollock. 1984. Effects of permanent trap response in capture probability on Jolly-Seber capture-recapture model estimates. *Journal of Wildlife Management* 48:289-294.
- Nichols, J. D., B. R. Noon, S. L. Stokes, and J. E. Hines. 1981. Remarks on the use of mark-recapture methodology in estimating avian population size. *Studies in Avian Biology* 6:121-136
- Noon, B. R., and C. M. Biles. 1990. Mathematical demography of spotted owls in the Pacific Northwest. *Journal of Wildlife Management* 54:18-27.
- Noon, B. R., and J. R. Sauer 1992. Population models for passerine birds: structure, parameterization, and analysis. Pages 441-464 in D. R. McCullough and R. H. Barrett, editors. *Wildlife 2001 Populations*. Elsevier Scientific Publishers, Ltd., London, England.
- Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107:1-97
- Pradel, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics* 52: 703-709.
- Rao, P. S. R. S. 1997. Variance components estimation: mixed models, methodologies and applications. Chapman and Hall, London, England.
- Sakamoto, Y., M. Ishiguro, and G. Kitagawa. 1986. Akaike information criterion statistics. KTK Scientific Publishers, Tokyo, Japan.
- SAS Institute. 1997. SAS/STAT® Software: changes and enhancements through release 6.12. SAS Institute, Inc., Cary, North Carolina, USA.
- Seber, G. A. F. 1965. A note on the multiple recapture census. *Biometrika* 52:249-259.
- Seber, G. A. F. 1982. Estimation of animal abundance and related parameters. Macmillan, New York, New York, USA.
- Skalski, J. R., A. Hoffmann, and S. G. Smith. 1993. Testing the significance of individual- and cohort-level covariates in animal survival studies. Pages 9-28 in J.-D. Lebreton and P. M. North, editors. *Marked individuals in the study of bird population*. Birkhäuser Verlag, Basel, Switzerland.

- Thomas, J. W., E. D. Forsman, J. B. Lint, E. C. Meslow, B. R. Noon, and J. Verner. 1990. A conservation strategy for the Northern Spotted Owl. Report of the Interagency Scientific Committee. U. S. Department of Agriculture - Forest Service, U. S. Department of Interior - Bureau of Land Management and Fish and Wildlife Service, and National Park Service. U.S. Government Printing Office 791-171/20026, Washington, D.C, USA.
- USDA and USDI. 1994. Final supplemental environmental impact statement on management of habitat for late-successional and old-growth forest related species within the range of the Northern Spotted Owl, 2 volumes. U. S. Department of Agriculture - Forest Service and U. S. Department of Interior - Bureau of Land Management, Portland, Oregon, USA.
- USDI. 1990. Endangered and threatened wildlife and plants: determination of threatened status for the Northern Spotted Owl. *Federal Register* 55:26114-26194.
- USDI. 1992. Final draft recovery plan for the Northern Spotted Owl, 2 Vols. U.S. Department of Interior, Washington, D.C., USA.
- White, G. C., and R. E. Bennetts. 1996. Analysis of frequency count data using the negative binomial distribution. *Ecology* 77:2549-2557.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study*. In Press.

APPENDIX A. List of participants at the workshop on analysis of demographic rates for the Northern Spotted Owl held 7-14 December 1998 in Corvallis, Oregon.

BIOLOGISTS WITH DEMOGRAPHIC DATA (listed by study area and state)

Cle Elum (Washington)

Stan Sovern	Forestry Sciences Lab, USDA Forest Service
Eric Forsman	Forestry Sciences Lab, USDA Forest Service

Olympic Peninsula (Washington)

Erran Seaman	Olympic National Park
Brian Biswell	Forestry Sciences Lab, USDA Forest Service
Eric Forsman	Forestry Sciences Lab, USDA Forest Service

Rainier (Washington)

Dale Herter	Raedeke Associates
-------------	--------------------

Wenatchee (Washington)

Tracy Flemming	National Council of Air & Stream Improvement
Larry Irwin	National Council of Air & Stream Improvement

Oregon Department of Forestry, Astoria Region (Oregon)

Amy Ellingson	Department of Fish and Wildlife, Oregon State University
Robert Anthony	Oregon Cooperative Wildlife Research Unit, Oregon State University

Elliot State Forest and Oregon Coast Range (Oregon)

Peter Loschl	Forestry Sciences Lab, USDA Forest Service
Keith Swindle	Oregon Cooperative Wildlife Research Unit, Oregon State University
Robert Anthony	Oregon Cooperative Wildlife Research Unit, Oregon State University
Eric Forsman	Forestry Sciences Lab, USDA Forest Service

East Eugene (Oregon)

Dennis Rock	National Council of Air & Stream Improvement
Larry Irwin	National Council of Air & Stream Improvement

H. J. Andrews (Oregon)

Jim Thrailkill	Oregon Cooperative Wildlife Research Unit, Oregon State University
Robert Anthony	Oregon Cooperative Wildlife Research Unit, Oregon State University

Roseburg BLM - Klamath (Oregon)

Joseph Lint	Bureau of Land Management
-------------	---------------------------

Roseburg BLM - Tye (Oregon)

Janice Reid Forestry Sciences Lab, USDA Forest Service
Eric Forsman Forestry Sciences Lab, USDA Forest Service

Southern Cascades (Oregon)

Frank Wagner Department of Fish and Wildlife, Oregon State University
Robert Anthony Oregon Cooperative Wildlife Research Unit, Oregon State University

Warm Springs Tribal Lands (Oregon)

Rick Gearhart Private Consultant

Hoopa Tribal Lands (California)

Mark Higley Hoopa Tribal Forestry
Billy Colgrove Hoopa Tribal Forestry
Jeff Dunk Redwood Sciences Laboratory, USDA Forest Service
Howard Stauffer Department Mathematics, Humboldt State University

Simpson Timber Company (California)

Lowell Diller Simpson Timber Company, Redwood Division
Rich Klug Simpson Timber Company, Redwood Division
Lee Foillard Simpson Timber Company, Redwood Division
Trent McDonald WEST, Inc.

NW California (California)

Peter Carlson Department of Wildlife, Humboldt State University
Alan Franklin Colorado Coop. Fish & Wildlife Research Unit, Colorado State University
R. J. Gutiérrez Department of Wildlife, Humboldt State University (NWC)

ANALYSTS/INSTRUCTORS

Mary Connor Department of Fishery & Wildlife Biology, Colorado State University
Jennifer Blakesley Colorado Coop. Fish & Wildlife Research Unit, Colorado State University
Kenneth Burnham Colorado Coop. Fish & Wildlife Research Unit, Colorado State University
Steven J. Dinsmore Department of Fishery & Wildlife Biology, Colorado State University
Alan Franklin Colorado Coop. Fish & Wildlife Research Unit, Colorado State University
James Hines Patuxent Wildlife Research Center, U.S. Geological Survey
James D. Nichols Patuxent Wildlife Research Center, U.S. Geological Survey
Greg Phillips Department of Fishery & Wildlife Biology, Colorado State University
Eric Rexstad Institute of Arctic Biology, University of Alaska - Fairbanks
Carl Schwarz Department of Statistics and Mathematics, Simon Fraser University
Tanya Shenk Colorado Division of Wildlife
Gary White Department of Fishery and Wildlife Biology, Colorado State University

OTHER ATTENDEES

Gina King Yakima Tribe

ORGANIZERS

David Anderson	Colorado Coop. Fish & Wildlife Research Unit, Colorado State University
Robert Anthony	Oregon Cooperative Wildlife Research Unit, Oregon State University
Kenneth Burnham	Colorado Coop. Fish & Wildlife Research Unit, Colorado State University
Eric Forsman	Forestry Sciences Lab, USDA Forest Service
Alan Franklin	Colorado Coop. Fish & Wildlife Research Unit, Colorado State University
Dan Rosenberg	Oregon Cooperative Wildlife Research Unit, Oregon State University
E. Charles Meslow	Wildlife Management Institute
Gary White	Department of Fishery and Wildlife, Colorado State University

APPENDIX B - Agenda of the Workshop on Analysis of Demographic Rates of Northern Spotted Owls, 7-14 December 1998.

MONDAY (7 Dec)

- All Day (Ken Burnham and Gary White)
 - Workshop Purpose & Goals
 - Overview of Capture-Recapture and program MARK

TUESDAY (8 Dec)

- Morning (Ken Burnham and Jim Nichols)
 - Estimation of θ
- Afternoon (Gary White and Ken Burnham)
 - Protocol Session

WEDNESDAY (9 Dec)

- All Day (Individual Studies)
 - Analysis of age-specific survival in MARK

THURSDAY (10 Dec)

- All Day (Individual Studies)
 - Analysis of age-specific survival in MARK
- Evening (Nichols/Hines/White/Franklin)
 - Assessment & query of data sets for estimating θ_{RJS}

FRIDAY (11 Dec)

- Morning (Nichols/Hines/White/Franklin)
 - Assessment & query of data sets for estimating θ_{RJS}
- Afternoon (Individual Studies)
 - Analysis of θ_{RJS} in MARK

SATURDAY (12 Dec)

- All Day (Individual Studies)
 - Analysis of θ_{RJS} in MARK

SUNDAY (13 Dec) - Day off

MONDAY (14 Dec)

- All Day (Everyone)
 - Clean up loose ends and compilation of data files and results; Departure

Fecundity Data

- 1) Differences between study areas because not every study followed the same protocols for collecting fecundity data. Two basic protocols: 4-mouse protocol and 2 visits (strict protocol), and <4-mouse and/or 1 visit (relaxed protocol). Consistent across study areas and years. Expect to miss young with fewer visits, particularly if no young are found. However, if more visits are used for sites with no young found, then the bias may not be important.

Resolution: categorize types of protocols and include a protocol fixed effect in the fecundity model, and evaluate whether this effect is needed with AIC model selection techniques. Recognize that protocol and study area are confounded, and that this confounding cannot be removed. Will not be able to show differences in fecundity between study areas with different protocols.

2. Missing fecundity data for a specific female (10-20% of records) -- gaps in breeding record. Bird is known to be alive, because a nest record is found for the bird in a later year. Is this missing data because the bird was not found, and can be assumed to be a random event (missing at random)? Need bird ID and site ID to tease out bird vs. site effects.

Non-breeding birds are assumed to be as easy to locate as breeding birds. Another analysis would be to develop a multi-strata model with strata of ≥ 1 young vs. 0 young. What would the impact (bias) be because birds may be incorrectly classified into the wrong strata.

Resolution: Approach 1: gaps will be replaced with a zero. Approach 2: gaps will be treated as missing value (missing at random, as done in 1993). Another possibility is to use the number of people monitoring per owl territory as a covariate. Consensus is to use same method as 1993 (approach 2). Only the estimate from approach 2 will be used in the Leslie matrix projection. Analysis this time will include protocol method as a fixed effect.

Analysis of age (J, S1, S2, and A) and sex data: estimates of N_j , N_{S1} , N_{S2} , and N_A .

This is Data Type A. \hat{c} will be provided from bootstrap goodness-of-fit values – table prepared by Alan Franklin.

Models to be estimated for N , where $a = \text{age}(J, S1, S2, A)$, $J = \text{Juvenile}$, $NJ = \text{non-juvenile}$, $s = \text{sex}$, $t = \text{time}$:

1. $\{N(a*s*t) p(a*s*t)\}$

Models to be crossed with all p models:

2. $N([J, [S1, S2, A]+s]+t)$ times $p(\text{all possible})$
3. $N([J, NJ+s]+t)$ times $p(\text{all possible})$

Models to be built based on best AIC model from ϕ X p models:

4. $N([J, NJ+s]+T)$ with p structure from best AIC model from 2-3 above
5. $N([J, NJ+s]+ln[T])$ with p structure from best AIC model from 2-3 above
6. $N([J, NJ+s]+[TT])$ with p structure from best AIC model from 2-3 above
7. best AIC model from 2-6 above, dropping s
8. best AIC model from 2-6 above, with $J(.)$

Models to be estimated for p ($a4'$ means birds initially banded as juveniles have different recapture rates than birds not initially banded as juveniles for the next 3 years after initial capture):

- 1) $p([a4'+s], [NJ+s+t])$
- 2) $p([a4'+s], [NJ+s+T])$
- 3) $p([a4', NJ]+s)$
- 4) 3 models of biologist's choice specific to study area

Total models to be estimated: 18.

Handling 2 different estimates of θ

θ_{RJS} reflects time-specific changes in rate of population change on study area, given that the size of the study area has not changed. Studies were not designed with using this model in mind, so that study area boundaries may have expanded. In addition, any trap happy response of birds, where recapture rates exceed initial capture rates, will cause θ_{RJS} to be biased high. θ_{PM} uses study area averages of fecundity and survival. If $N(t)$ model is the best AIC model, the variance components (random effects) estimate of average N will be used. If $N(T)$ model results, the trend will be centered and then the intercept will be the average N . The value of $\hat{\lambda}_{PM}$ is expected to be biased negatively, because survival estimates plugged into the Leslie matrix are apparent survival [$N = S(I - E)$].

Decision: compute both estimates for study areas where the RJS assumptions are reasonably met, and report these estimates. θ_{PM} will be done for all study areas to compare with the 1993 estimate. The decision to compute θ_{RJS} is made for each study area. We want to examine the difference in the estimates. Recognize that we don't fully understand the behavior of θ_{RJS} , and discuss the potential problems and caveats of this approach.

Criteria to decide whether a study area has θ_{RJS} computed:

- 1) Investigators are willing to do the analysis for their data, i.e., they think that their data approximately meet the assumptions of the method;
- 2) Study area has not been steadily expanded across time.

Models for θ_{RJS} :

- 1) $\delta_{RJS}(\cdot)$
- 2) $\delta_{RJS}(T)$
- 3) $\delta_{RJS}(TT)$
- 4) $\delta_{RJS}(\text{Threshold or } \ln(T))$
- 5) $\delta_{RJS}(t)$

Use best AIC model from Data Type A for recapture rates, p , from adult females. Model for ϕ will be $N(t)$.

Estimation of δ_{PM}

Repeat analysis for δ_{PM} as in 1993 with updated estimates of radio-tracking juvenile emigration rates from 3 study areas. Estimates of juvenile emigration will only be used with 3 study areas where the data were collected. For other study areas where no juvenile emigration rates are known, estimates of juvenile emigration rates required to obtain $\delta = 1$ will be determined. Likewise, holding juvenile survival constant, the amount of change in adult emigration will be determined to obtain $\delta = 1$ for each study area, because no study area has estimates of adult emigration. A third analysis will be to put in the “best guess” for juvenile emigration from observed values from 3 study areas, and then evaluate the adult emigration rate to obtain $\delta = 1$. Generate a graph of solutions for $\delta = 1$ with x-axis of juvenile emigration, and y-axis of adult emigration.

Adult female meta-analysis on 15 study areas.

Point of analysis is to examine consistency of adult female survival rates across study areas. Encounter histories will be extracted from Data Type A encounter history matrices.

Models to be estimated:

- 1) $N(g*t)$
- 2) $N(g+t)$
- 3) $N(g*T)$
- 4) $N(g+T)$
- 5) $N(\text{province*best from 1-4 above})$ with p structure from best AIC model
- 6) $N(\text{ownership*best from 1-4 above})$ with p structure from best AIC model
- 7) $N(\text{province*ownership*best from 1-4 above})$ with p structure from best AIC model
- 8) $N(G[\text{latitude}]*\text{best from 1-4 above})$ with p structure from best AIC model

Province and ownership are categorical variables. Categories of province are:

Province Category

Study Areas

East Slope Cascades Douglas Fir/Hemlock	CLE, WEN, WSR, AST, OLY, RAI, HJA, ELC, EEU, TYE
Mixed Conifer/Hardwood/Frank's Area Redwood	CAS, NWC, KLA, HUP, SIM

<u>Ownership Category</u>	<u>Study Areas</u>
USFS/NPS	CAS, HJA, NWC, OLY
Mixed	ELC, KLA, TYE, EEU, CLE, RAI, WEN
Non-Federal	AST, HUP, WSR, SIM,

Models for p:

- 1) $p(g^*t)$
- 2) $p(g+t)$
- 3) $p(g^*T)$
- 4) $p(g+T)$

Total models: 20.

Adult female meta-analysis on 8 monitoring areas (CAS, CLE, COA, HJA, KLA, NWC, OLY, TYE).

Point of analysis is to examine consistency of adult female survival rates across study areas. Encounter histories will be extracted from Data Type A encounter history matrices.

Models to be estimated:

- 1) $N(g^*t)$
- 2) $N(g+t)$
- 3) $N(g^*T)$
- 4) $N(g+T)$
- 5) $N(\text{province}^*\text{best from 1-4 above})$ with p structure from best AIC model
- 6) $N(\text{ownership}^*\text{best from 1-4 above})$ with p structure from best AIC model
- 7) $N(\text{province}^*\text{ownership}^*\text{best from 1-4 above})$ with p structure from best AIC model
- 8) $N(G[\text{latitude}]^*\text{best from 1-4 above})$ with p structure from best AIC model

Province and ownership are categorical variables. Categories of province are:

<u>Province Category</u>	<u>Study Areas</u>
East Slope Cascades	CLE

Douglas Fir/Hemlock	OLY, HJA, COA, TYE
Mixed Conifer/Hardwood/Frank's Area	CAS, NWC, KLA

<u>Ownership Category</u>	<u>Study Areas</u>
USFS/NPS	CAS, HJA, NWC, OLY
Mixed	COA, KLA, TYE, CLE

Models for p:

- 1) $p(g^*t)$
- 2) $p(g+t)$
- 3) $p(g^*T)$
- 4) $p(g+T)$

Total models: 20.

INVESTIGATION OF BIAS IN THE FACE OF ASSUMPTION VIOLATIONS

We consider three specific kinds of assumption violations: expansion of study area over time, permanent trap response in capture probability, and heterogeneous capture probabilities. We also investigated the combined effects of trap response and heterogeneity.

Expansion of study area over time.

One potential problem involves expansion of the study area over time. The sampling situation envisioned involves beginning with a well-defined study area. However, while sampling the study area, investigators may locate birds near the defined study area, yet slightly beyond study area boundaries. As such birds are detected, they are added to the marked sample, and recapture efforts in subsequent years include visits to these particular territories, despite the fact that they lie outside the initial study area boundaries. Thus, the investigators are essentially sampling a larger area, and the population of owls within this additional area, as the study progresses.

This sampling situation does not produce bias, in the sense that the estimator of λ_i is not performing as it was intended. Instead, the area being sampled is increasing, so the estimated population change is the result of two conceptually distinct processes. The first process involves changes in the number of birds on the sampled area; this is the change of interest and the one to which we would like $\hat{\lambda}_i$ to apply. The second process involves expansion of the study area and the increase in number of birds exposed to sampling that result from this expansion.

If we view the change in number of birds on the originally defined study area as the true quantity of interest, then we can consider the “bias” in $\hat{\lambda}_i$ associated with study area expansion. Let N_i denote the number of animals exposed to sampling efforts on the original study area. Then the true parameter of interest is $\lambda_i = N_{i+1}/N_i$. Let N'_i be the number of birds exposed to sampling efforts during year i that were not exposed to sampling efforts during year $i-1$ (these birds are associated with the new area sampled in year i). If we view $\hat{\lambda}_i$ as the rate of increase estimated from sampling efforts, then we should be able to approximate relative bias in $\hat{\lambda}_i$ as:

$$\text{Bias}(\hat{\lambda}_i) = E(\hat{\lambda}_i) - \lambda_i \approx \frac{N_{i+1} + N'_{i+1}}{N_i} - \frac{N_{i+1}}{N_i} = \frac{N'_{i+1}}{N_i} \quad (1)$$

Relative bias in $\hat{\lambda}_i$ is thus given by:

$$\text{Rbias}(\hat{\lambda}_i) = \frac{E(\hat{\lambda}_i) - \lambda_i}{\lambda_i} \approx \frac{N'_{i+1}}{N_{i+1}} \quad (2)$$

The interpretation of (2) is that the relative bias of $\hat{\lambda}_i$ is given by the proportional increase in the number of birds exposed to sampling efforts resulting from the expansion of study area in time $i+1$, relative to the area sampled in time i .

Regarding application of this method of estimating λ_i , the recommendation is simply to restrict use of this approach to sampling situations where study area expansion is negligible. In situations where this expansion has occurred, it may be possible to restrict analyses to a subset of

the data. Perhaps the important thing to remember about this approach to estimating λ_i is that it estimates the rate of change in abundance of birds exposed to sampling efforts. If this quantity reflects population dynamics of birds, then it will likely be of interest to us, whereas if it reflects both population dynamics and changes in sampling (e.g., area expansion), then biological interpretation may be more difficult.

Permanent trap response in capture probability.

Another aspect of spotted owl sampling that may influence utility of $\hat{\lambda}_i$ for drawing inferences about owl populations involves the general issue of permanent trap response. A standard approach to owl sampling seems to involve a change in sampling once a territorial bird has been encountered for the first time. In all years following initial location and capture, investigators return to the specific territory (sometimes multiple times) insuring that capture probability is very high for marked birds. However, it is likely that capture probability for birds that have not been previously marked will be lower, perhaps substantially so. The term “trap response” was originally intended to apply to an animal’s response to being captured (e.g., Seber 1982), whereas our application of the term here applies to a change in capture probability induced by investigator behavior, rather than bird behavior. We retain the terminology, because it reflects a difference in capture probability between birds that have, and have not, been previously marked, and this difference in capture probability is the quantity of relevance here.

The influence of permanent trap response in the standard Cormack-Jolly-Seber modeling context has been investigated and shown to induce no bias in survival estimates. This was expected because survival estimates are conditional on animals that are captured, so all modeled capture probabilities correspond to marked birds. Estimates of population size under the Jolly-Seber model, however, are biased in the face of permanent trap response, as the difference in capture probability between marked and unmarked causes predictable problems (e.g., see Nichols et al. 1984).

Our initial intuition about this problem led us to believe that $\hat{\lambda}_i$ would likely be positively biased in the face of trap response. We will provide a skeleton argument of that reasoning here. One line of evidence simply involves the definition of λ_i as N_{i+1}/N_i . If permanent trap response results in biased estimates of abundance, then it seems reasonable that it might cause problems in the estimation of λ_i , although this line of reasoning does not yield an inference about direction of any resulting bias. The inference about directionality of bias emerges from a consideration of an alternative parameterization of the reparameterized Jolly-Seber model. The relationship between the λ parameterization and the γ parameterization can be written as:

$$\lambda_i = \frac{\phi_i}{\gamma_{i+1}} \quad (3)$$

where these parameters have been defined above. Although the survival estimate under the Cormack-Jolly-Seber model is unbiased in the face of permanent trap response, we believe that the $\hat{\gamma}_i$ are likely to be negatively biased.

We can think of the $\hat{\gamma}_i$ as estimating the fraction of animals present at i that were also present at time $i-1$. This estimation involves the number of animals actually caught in times i and $i-1$. In order to estimate the actual number of animals present in both periods, we can divide

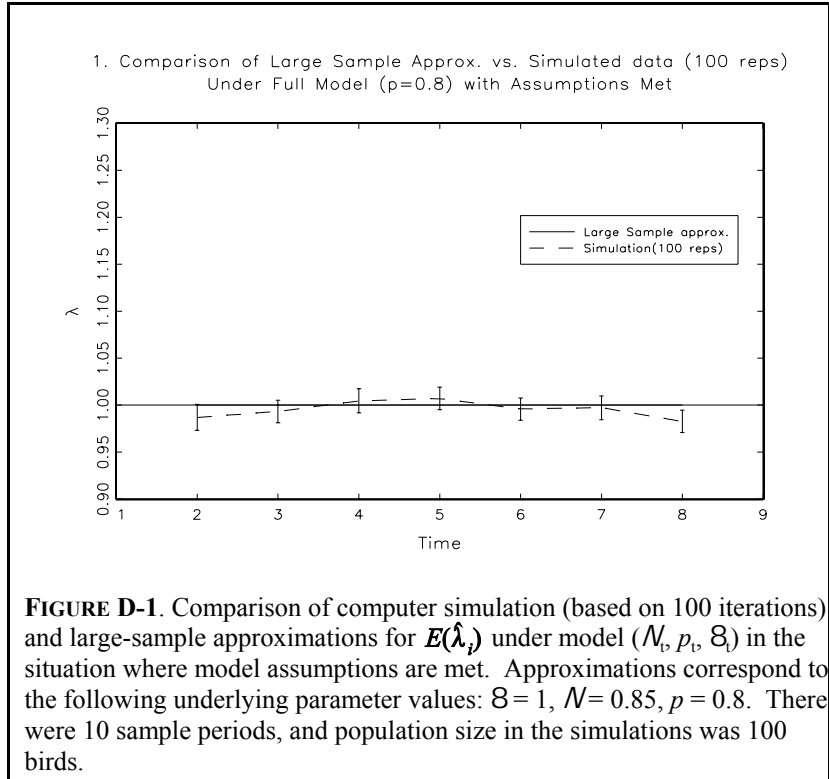
the number observed in both periods by the estimated capture probability at time $i-1$, \hat{p}_{i-1} (note that the maximum likelihood estimation does not actually work in this way, but this is an *ad hoc* estimation approach that can perhaps provide insight into the process). However, most of the information for estimating \hat{p}_{i-1} comes from recaptures (not new captures of unmarked animals). If recapture probability is really larger than capture probability of unmarked animals, then the \hat{p}_{i-1} will apply approximately to animals marked before $i-1$ (M_{i-1}) but not to the remainder of animals available for capture at $i-1$ ($N_{i-1} - M_{i-1}$). When \hat{p}_{i-1} is too large for some fraction of the animals present at $i-1$, then the estimates of γ_i will be too small. Because of the relationship in (3), the $\hat{\lambda}_i$ will show positive bias.

We examined the influence of permanent trap response on estimates of λ_i using both large-sample analytic approximations and computer simulation (e.g., Nichols et al. 1981, Burnham et al. 1987). The large-sample approximations were obtained by computing the expected value of each observable capture history under a specified set of parameter values. We considered the situation of 10 sampling periods. We used 100,000 or 200,000 animals as a population size in order to insure sufficiently large numbers of animals exhibiting each capture history to permit a reasonable approximation (because we submitted integer numbers to the data-analytic program, MARK). Expected population size was constant over time (i.e., we assumed true $\mathcal{S}_i = 1$), and this was accomplished by adding to the population each time period a number of new unmarked animals equal to the number of expected deaths (additions equaled $N(1 - \mathcal{M})$, where N is the population size and \mathcal{M} is the local survival probability). We used a survival rate of $\mathcal{M} = 0.85$ for all approximations. The expected values of the capture histories were submitted as data to program MARK, and the resulting parameter estimates are approximations to $E(\hat{\lambda}_i)$. We approximated $E(\hat{\lambda}_i)$ under three different models, model ($\mathcal{N}_b, p, \mathcal{S}$), model ($\mathcal{N}_b, p, \mathcal{S}_b$), and model ($\mathcal{N}_b, p_b, \mathcal{S}_b$).

In addition to these large-sample approximations, we used computer simulation to approximate $E(\hat{\lambda}_i)$ for small population and sample sizes similar to those encountered in spotted owl studies. In these simulations we generated capture history data with individual survival and capture both treated as stochastic processes (Bernoulli trials). For most simulations, we used 100 as a population size. Additions of new animals were treated in a deterministic (rather than stochastic) manner, as we added the number of individuals each time period needed to compensate for the expected number of deaths ($N(1 - \mathcal{M})$, where N is the initial population size). Again, a survival rate of $\mathcal{M} = 0.85$ was used in all simulations, and $E(\mathcal{S}) = 1$. For each scenario, we conducted 100 iterations and estimated the expected value of $\hat{\lambda}_i$ as the mean of the 100 different parameter estimates. We approximated $E(\hat{\lambda}_i)$ in this manner for two models, model ($\mathcal{N}_b, p, \mathcal{S}$), and model ($\mathcal{N}_b, p_b, \mathcal{S}_b$). As in the large-sample approximations, we considered the case of 10 sample periods.

We investigated several different scenarios for trap response by specifying different values for the capture probabilities of unmarked (p) and previously marked (c) birds. We set the capture probability for previously marked birds as $c = 0.8$ in all scenarios. We investigated values for capture probability of unmarked birds ranging from $p = 0.1$ to 0.9 in increments of 0.1 . These different scenarios included extreme levels of “trap-happy” response (e.g., $p = 0.1$, $c = 0.8$) as well as an example of a “trap-shy” response ($p = 0.9$, $c = 0.8$), to include the situation of marked owls avoiding capture efforts.

The values of $E(\hat{\lambda}_i)$ obtained using large-sample approximations and computer simulation showed good agreement both for the case of no trap response (underlying model assumptions were met, Fig. D-1) and substantial trap-happy response (Fig. D-2). Because of this agreement, we present primarily large-sample approximations. As predicted, $E(\hat{\lambda})$ under model (N, p, δ) shows a positive bias in the presence of a trap-happy response (Fig. D-3). The approximate relative bias of $\hat{\lambda}$ ranged from about 0.10 for $p = 0.1$ and $c = 0.8$ to < 0.01 for $p = 0.7$ and $c = 0.8$. The trap-shy response of $p = 0.9$ and $c = 0.8$ yielded a small negative bias in $\hat{\lambda}$.



The time-specific approximations for $E(\hat{\lambda}_i)$ showed an interesting (and potentially misleading) temporal trend, as $E(\hat{\lambda}_i)$ decreased over time (Fig. D-4). $E(\hat{\lambda}_i)$ was largest in sampling period 2 (relative bias of approximately 0.28 for $\hat{\lambda}_2$ in the case of $p = 0.1$ and $c = 0.8$) and decreased monotonically to values near 1 for later sampling periods (Fig. D-4). As was the case for the constant-parameter model, bias was not substantial for small levels of trap response, although some evidence of a trend was present for all degrees of trap response investigated. The trend in $E(\hat{\lambda}_i)$ was positive in the case of a trap-shy response.

An *a posteriori* explanation for the trend in $E(\hat{\lambda}_i)$ involves changes in the relative numbers of marked and unmarked animals in the population through time. The intuitive explanation about the expectation of positive bias in $\hat{\lambda}_i$ under a trap-happy response involved the inappropriate application of capture probability parameters that were based primarily on recaptures to unmarked animals. Unmarked animals comprise a larger proportion of the population in the early periods, whereas marked animals come to dominate the later periods. Thus the greater bias in the earlier time periods is consistent with this line of reasoning.

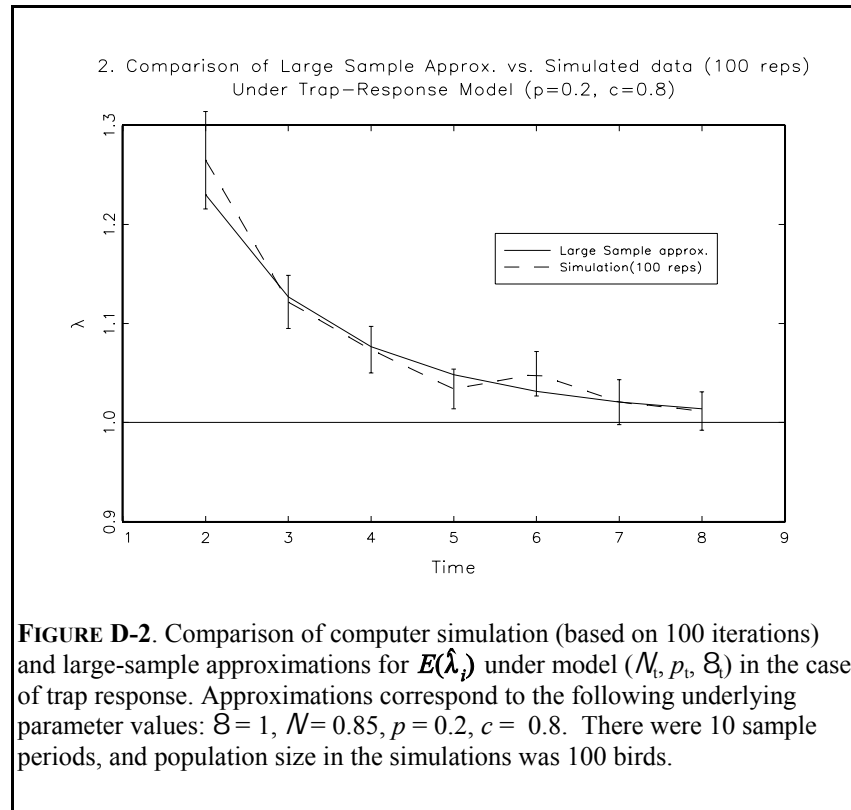
Heterogeneous capture probabilities.

Another potential problem involved heterogeneous capture probabilities among individuals. In this situation, different individuals were assumed to have different capture probabilities. However, these probabilities were assumed to remain constant within individuals throughout the study (no temporal variation or trap response). Different investigators had

different intuitions and *a priori* expectations for the results of this analysis. Some expected substantial bias with heterogeneity perhaps producing effects similar to those induced by trap response. Others argued that although heterogeneity produces substantial negative bias in individual estimates of population size, parameters (such as λ_i) reflecting ratios of population size should not be badly affected.

As with the numerical investigations of trap response, we used both large-sample approximations and computer simulation to investigate $E(\hat{\lambda}_i)$. We modeled heterogeneity using a simple 2-group distribution (e.g., see Carothers 1973). The large-sample approximations were computed in the same general manner as for trap response. Instead of having different capture probabilities corresponding to marked/unmarked status, we generated expected numbers of animals in the different capture histories using 1 capture probability (p^1) for a constant population of 100,000 birds and a different capture probability (p^2) for a different population of 100,000 birds. These capture probabilities remained the same for birds throughout their lives and did not change with mark status, for example. The number of additions to the population each year was set equal to the expected number of deaths ($N(1 - \mathcal{M})$), so the entire population of 200,000 birds remained approximately constant over time ($\mathcal{S} = 1$). As in the numerical work on trap response, a survival rate of $\mathcal{N} = 0.85$ was used for these approximations. The capture histories for the two groups were combined to yield expected capture histories with heterogeneous capture probabilities for the total population of 200,000 birds. We again considered studies with 10 annual sample periods. As in the investigation of trap response, we approximated $E(\hat{\lambda}_i)$ under three different models, model $(\mathcal{N}_t, p_., \mathcal{S}_i)$, model $(\mathcal{N}_t, p_., \mathcal{S}_i)$, and model $(\mathcal{N}_t, p_t, \mathcal{S}_i)$.

In the computer simulation approach, we used 50 birds in each of the two groups (the groups defined by capture probabilities p^1 and p^2) and treated individual survival and capture as Bernoulli trials. For each subgroup, we added new individuals to equal the expected number of deaths in the group each time period ($N(1 - \mathcal{M})$), so $E(\mathcal{S}) = 1$. The capture histories for the two groups were combined to yield the data for a heterogeneous population of 100 birds. We estimated λ under two models, $(\mathcal{N}_t, p_., \mathcal{S}_i)$ and $(\mathcal{N}_t, p_t, \mathcal{S}_i)$.



We investigated different scenarios reflecting different degrees of heterogeneity. We retained $p^1 = 0.9$ for the high- p group in all scenarios, and we set $p^2 = 0.1, 0.2, \dots, 0.9$ for the low- p group. We first compared the computer simulation and large-sample approximations of $E(\hat{\lambda}_i)$ for the scenario of $p^2 = 0.9, p^1 = 0.2$ under model (N, p, δ) . The approximations using these two alternative approaches showed good agreement (Fig. D-5).

Large-sample approximations for $E(\hat{\lambda})$ under model (N, p, δ) showed no evidence of bias (i.e., $E(\hat{\lambda})=1.00$), indicating

no influence of heterogeneous capture probabilities on estimates of δ under this model. However, the time-specific estimates of λ under model (N, p, δ) did show evidence of bias, with approximations of bias ranging from -0.05 to 0.05 for the individual $\hat{\lambda}_i$ (Fig. D-6). Interestingly, the time-specific approximations for $E(\hat{\lambda}_i)$ showed a temporal trend, as $E(\hat{\lambda}_i)$ decreased over time (Fig. D-6). The magnitude of bias was dependent on the degree of heterogeneity, although the greatest bias was not observed for the largest degree of heterogeneity. Instead, the greatest bias was associated with the scenario of $p^1 = 0.9, p^2 = 0.3$, whereas the scenario of $p^1 = 0.9, p^2 = 0.1$ showed smaller bias. An *a posteriori* explanation for this difference, is that when the low- p group has a sufficiently low capture probability, these birds provide a small contribution to the capture history data, leaving most data corresponding to birds in the high- p group.

Heterogeneous capture probabilities do not appear to present as substantial a problem as does permanent trap response in capture probabilities. Bias in $\hat{\lambda}$ appears to be negligible under model (N, p, δ) , and bias in the $\hat{\lambda}_i$ under model (N, p, δ) is relatively small. The time-specific model also showed a temporal trend in bias of $\hat{\lambda}_i$.

Combined Effects of Trap Response and Heterogeneity.

It is certainly possible that permanent trap response and heterogeneity could be operating simultaneously in a sampled population. Specifically, we envisioned two groups of birds (1 and 2) with different capture probabilities for unmarked (p^1, p^2) and marked (c^1, c^2) birds within each group. We investigated this possibility using large-sample approximations as described above. We retained a constant population of 100,000 in each group of birds and again used an annual

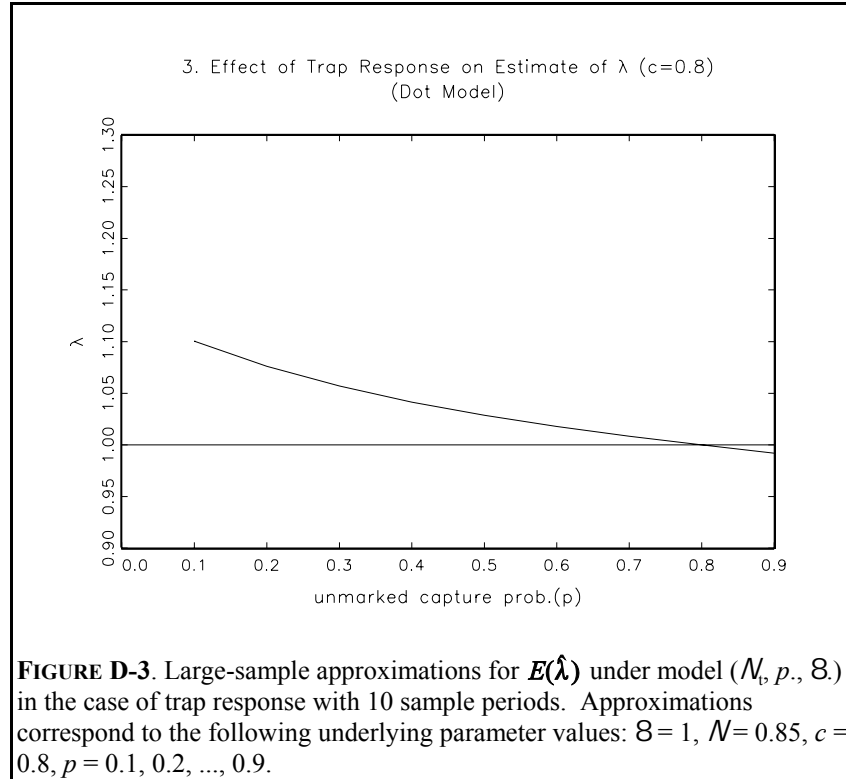


FIGURE D-3. Large-sample approximations for $E(\hat{\lambda})$ under model (N, p, δ) in the case of trap response with 10 sample periods. Approximations correspond to the following underlying parameter values: $\delta = 1, N = 0.85, c = 0.8, p = 0.1, 0.2, \dots, 0.9$.

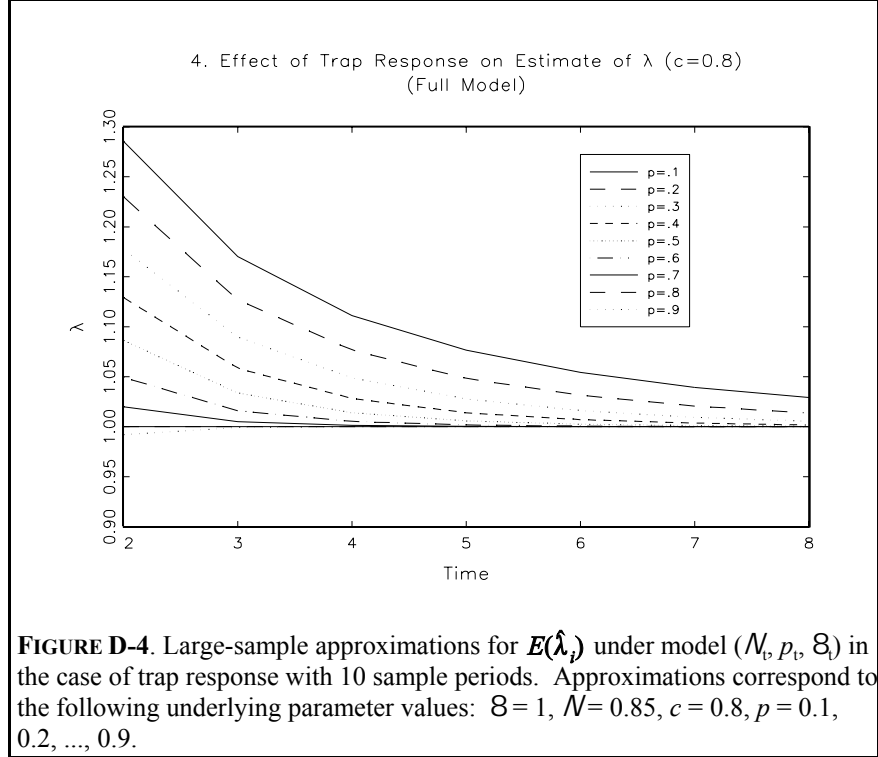
survival probability of 0.85. We computed approximations for $E(\hat{\lambda}_t)$ under models (N_t, p_t, δ_t) , (N_t, p_t, δ_t) , and (N_t, p_t, δ_t) .

We left capture probabilities for group 2 the same for all scenarios at $p^2 = 0.4$, $c^2 = 0.9$. We then defined different scenarios using the following capture probabilities for members of group 1: $p^1 = 0.1$, $c^1 = 0.6$; $p^1 = 0.2$, $c^1 = 0.7$; $p^1 = 0.3$, $c^1 = 0.8$; $p^1 = 0.4$, $c^1 = 0.9$; and $p^1 = 0.45$, $c^1 = 0.95$.

Large-sample approximations for $E(\hat{\lambda}_t)$ under model (N_t, p_t, δ_t) show positive bias of approximate magnitudes

0.05 to 0.06 similar to those observed under some magnitudes of trap response (Fig. D-7).

Large-sample approximations for $E(\hat{\lambda}_t)$ under model (N_t, p_t, δ_t) show a temporal trend with decreases over time (Fig. D-8).



Bias and modeling considerations.

These bias investigations lead to a greater concern for trap response in capture probabilities than for heterogeneity. Of particular relevance to the modeling of population growth is the temporal trend in $\hat{\lambda}_t$ that can be generated by these violations of the assumption of equal capture probabilities (both trap response and heterogeneity). We thus tended to focus on full time-specific models (e.g., N_t, p_t, δ_t) and on models with time-invariant population growth (e.g., N_t, p_t, δ_t and N_t, p_t, δ_t). In the case of models with time-specific parameters, it may also be wise to view the initial estimate of population growth (usually $\hat{\lambda}_2$) with caution, as this estimate is likely to exhibit substantially greater bias than any subsequent estimates.

ESTIMATION AND MODELING OF λ_i : TECHNICAL NOTES

Pradel (1996) briefly describes estimation of \mathcal{S}_i under the reparameterized Jolly-Seber model. As with the standard Cormack-Jolly-Seber approach, some parameters are not separately estimable. For example, under model $(N_t, p_t, \mathcal{S}_t)$ with k sample periods, p_1 and \mathcal{S}_1 cannot be estimated separately but can be estimated as the ratio, λ_1/p_1 . Similarly, the final survival rate (N_{k-1}), capture probability (p_k), and population growth rate (\mathcal{S}_{k-1}) cannot be separately estimated, but are confounded with each other in two product parameters ($N_{k-1}p_k, \mathcal{S}_{k-1}p_k$). We can thus estimate $k-2$ survival probabilities, $k-2$ capture probabilities, $k-3$ population growth rates, and three combination parameters, yielding $2(k-2) + (k-3) + 3 = 3k-4$ parameters. Under model (N_t, p_t, γ_t) , which is simply a different parameterization of model $(N_t, p_t, \mathcal{S}_t)$, we can estimate $k-2$ parameters corresponding to survival probability, capture probability and seniority probability. We can also estimate two product parameters, $(\gamma_1, N_{k-1}p_k)$, again yielding $3(k-2) + 2 = 3k-4$ parameters.

Program MARK permits estimation under reduced-parameter models using all three parameterizations of the Pradel (1996) models. We view the γ_t parameterization as the most “natural” of these three. The f and λ parameterizations are artificial, in a sense, as they are written as functions of both γ and N . However, the f and λ parameters reflect quantities of substantial biological interest, and they are thus “natural” parameters in a biological sense. Because of the functional relationships among parameters, when we constrain f or λ parameters, we are simultaneously imposing constraints on survival and capture probabilities in a manner that is not always obvious. Consider the models $(N_t, p_t, \mathcal{S}_t)$ and (N_t, p_t, γ_t) in which λ and γ , respectively, are constrained to be constant over time. Under model (N_t, p_t, γ_t) , the constant γ permits estimation of p_1 , but the product parameter, $N_{k-1}p_k$, still remains, yielding $2k-1$ parameters. However, under model $(N_t, p_t, \mathcal{S}_t)$, p_1, p_k , and N_{k-1} are all estimable, yielding $2k$ parameters.

